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UNIVERSITY OF ALBERTA

IMPACT OF ENVIRONMENTAL FACTORS ON LIFE-HISTORY STRATEGIES OF THE MARINE POLYCHAETE *CAPITELLA* SP.

BY

PEI-YUAN QIAN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA, CANADA

FALL 1991

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University of Alberta
Edmonton

Canada T6G 2J9

Faculty of Graduate Studies and Research

2-8 University Hall, Telephone (403) 432-3499

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Subj: PhD thesis by P.Y. Qian

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Fred S. Chia
Supervisor of Mr. Qian.

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PERMANENT ADDRESS:

1# (C) Longshan Road, Qingdao

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled IMPACT OF ENVIRONMENTAL FACTORS ON LIFE-HISTORY STRATEGIES OF THE MARINE POLYCHAETE *CAPITELLA* SP. submitted by PEI-YUAN QIAN in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Dr. F. S. Chia (Supervisor)

Dr. A. N. Spencer

Dr. H. F. Clifford

Dr. D. A. Craig

Dr. W. J. Gallin (Committee chairman)

Dr. C. O. Hermans

Date May 28, 1991

ABSTRACT

Capitella sp., collected from subtidal squid egg mass and intertidal mudflats, showed differences in adult size, fecundity, egg size, egg energy content, total reproductive output, and developmental modes. By monitoring the reproductive events individually and by manipulating food conditions (quantity and quality) experimentally, it was demonstrated that some of these differences were mediated by diet. It was also discovered that fecundity, egg size, egg energy content, and total reproductive output of both planktotrophic and lecithotrophic developers decreased with age. The fecundity of lecithotrophic developers increased with increasing food quantity, but egg size and egg energy content decreased, whereas in planktotrophic developers, rate of sexual maturity, growth rate, and fecundity increased with increasing food quantity, but egg size decreased. In both planktotrophic and lecithotrophic developers, food quality affected growth rate, sexual maturity, spawning, fecundity, egg size and energy content, and total reproductive output.

Evidence was presented that the "morphological females" were in fact functional hermaphrodites since they developed ovaries and testes and stored sperm in the coelomoducts. Self-fertilization occurred, probably in the coelomoducts.

This study showed that fecundity, egg size, egg energy content, and larval development varied greatly among the siblings of a single spawn. Reproductive characteristics of *Capitella* sp. were flexible and could be modified by food conditions. It was suggested that many life-history models of marine invertebrates based on the simple assumption that reproductive characteristics in a given species remain constant should be re-evaluated. It was also suggested that the classifications of sibling species of marine invertebrates, when based largely on reproductive characteristics between populations, should be carefully re-considered.

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CHAPTER I

GENERAL INTRODUCTION

A. GENERAL LITERATURE REVIEW

In life history studies, the number and quality of offspring are frequently used as indicators of parental fitness. Both fecundity and offspring quality (egg size and energy content) are believed to describe the reproductive success of an individual. Therefore, a central issue in reproductive ecology is to know how a species maximizes its reproductive output in different environments. A basic assumption underlying the study of life history strategy is that natural selection acts on the number of offspring, the quality of offspring or both, in ways that maximize an organism's lifetime reproductive output. By definition, for Darwinian selection to operate on any of these reproductive characteristics, there must exist heritable variation among individuals. In fact, interspecific variations in the fecundity among individuals or populations of both vertebrates and invertebrates have been well documented (Lack 1954, Lack 1967, Bengston 1971, Kuznetsov 1973, Bayne *et al.* 1978, 1983, McKillup and Butler 1979, Krapu 1979, Brambilla 1982, Thompson 1982, Lewis and Storey 1984, MacDonald and Thompson 1985, 1986, Duncan 1986, Levin 1986, Levin and Creed 1986, Kaev and Kaeva 1986, Levin *et al.* 1987, Langton *et al.* 1987, Barber *et al.* 1988, Grémare *et al.* 1988, 1989a, 1989b, Henrich 1988, Boag 1989, Verity and Smayda 1989). All of these indicate that the number of offspring may be affected not only by the direct investment in each offspring, but also by the total resources available to the parents, and the fraction of these resources devoted to reproduction.

In both vertebrates and invertebrates, egg size has been widely used as an indicator of offspring size and quality. This practice is based on the assumption that egg size is correlated with parental investment per offspring, offspring size, and developmental type (Thorson 1946, 1950, Hermans 1966, Mileikovsky 1971, Vance

1973a, 1973b, Chia 1974, Christiansen and Fenchel 1979, Strathmann 1977, 1980, Strathmann and Vedder 1977, Caswell 1981, 1982, Winkler and Wallin 1987). In recent years, optimal models were proposed that suggested that parental fitness is maximized by investing equally in all young; therefore, selection should favor production of offspring of equal size (Smith and Fretwell 1974, Lloyd 1987, McGinley *et al.* 1987); also selection acts directly on offspring size that shows little intraspecific variation (Lloyd 1987). However, many studies have reported that variation in egg size is adaptive in vertebrates (Preston 1958, Festing and Nordskog 1967, Bagenal 1969, 1971, Coulson *et al.* 1969, Parsons 1972, Davis 1975, Vaisanen 1977, Brooke 1978, Crump and Kaplan 1979, Krapu 1979, Crump 1981, Lee 1981, Runde and Barrett 1981, Sharp and Moss 1981, Beckerton and Middleton 1982, Grant 1982, Furness 1983, Kuznetsov 1973, Thomas 1983, Kaplan and Cooper 1984, Loman 1984, Duncan 1986, Kaev and Kaeva 1987, Boag 1989). All of these authors support the hypothesis that variation in offspring size is a function of uncertainty of unstable environment, and that organisms tend to produce a wide range of egg size rather than a uniform size. In contrast to vertebrates, variation in egg size has not been carefully examined in marine invertebrates; such variation has been reported in only a few species (Barnes and Barnes 1965, Bayne *et al.* 1975, Turner and Lawrence 1979, McEdward and Carson 1987, McEdward and Coulter 1987). To my knowledge, variations in egg size and quality under controlled conditions have not been examined.

When considering the significance of intraspecific variations in fecundity and egg size, one of the major challenges is to determine how much of this variability is environmentally induced. In most previous studies, the results were based on observations of wild populations from different habitats or with different reproductive seasons. In such cases, it is difficult to define the effects of environmental factors on variations in either fecundity or egg size. Under controlled laboratory conditions, factors such as food quality, food quantity, and age can be manipulated and appropriate data on

the relationship between environmental conditions and fecundity and egg size can be expected.

Many previous models have predicted that there is a general trend for organisms in disturbed or unpredictable environments to show greater plasticity in life history traits; however, some of the hypotheses have been contradictory. One hypothesis is that, in an unpredictable and fluctuating environment, selection should favor production of as many offspring as possible, thus resulting in small-sized offspring (Hermans 1966, Pianka 1970, Schroeder and Hermans 1975, Kaplan 1979, Crump 1984, 1989). This hypothesis was supported by the fact that the egg size has no effects on larval survival rate, developmental time, or size at metamorphosis (Crump 1984). In this case, it is advantageous for the animal to produce more but smaller eggs. Another hypothesis has been proposed that in fluctuating or unpredictable environmental conditions, selection should favor production of fewer, but larger, eggs (Chia 1974, Nussbaum 1981, Nussbaum and Schultz 1989). This is based on the assumptions that larger eggs would develop into offspring that are more competitive for food and space, less vulnerable to predators, and that would, consequently, have better survival; these assumptions have been supported by many studies (Blaxter and Hempel 1963, Blaxter 1969, Bagenal 1969, Reagan 1977, Kaplan 1980a, 1980b, Kraeuter *et al.* 1982, Furness 1983, Kaplan and Cooper 1984, Marsh 1984, 1986, Duncan 1986, Henrich 1988, Rhymer 1988, Durate and Alcaraz 1989, Williamson and Bull 1989), in which it was demonstrated that larger eggs would result in higher survival rate.

B. SELECTION OF *CAPITELLA* SP. AS THE EXPERIMENTAL ANIMAL

Capitella sp. (Fig. I-1) found in the Bamfield area was used as the experimental animal. Here, it should be pointed out, that the morphological features of *Capitella* sp. were similar to those of the original description of *Capitella capitata* Fabricius 1780.

Figure I-1: Female of *Capitella* sp. collected from an intertidal mudflat in Grappler Inlet, Bamfield, British Columbia, Canada.

However, recent studies have divided *C. capitata*, collected from the United States, into ten sibling species (Grassle and Grassle 1976, Grassle 1980), although none of these sibling species have been defined properly. Therefore, *C. capitata* is presently no longer a functional species. Also the reproductive characteristics of *Capitella* sp. studied here do not fit the description of any sibling species reported by Grassle and Grassle (1976). Thus, it is proper for me to use the name *Capitella* sp. rather than *C. capitata*. Despite of problems in taxonomy, *Capitella* sp. makes an excellent study animal for four reasons. First, *Capitella* sp. meets all of the criteria necessary for a comprehensive life-history study in that it is very easy to culture and manipulate in the laboratory (maintenance of a large and healthy population doesn't require sophisticated techniques and equipment). Reproduction occurs year around, so research is not limited to the breeding season. It is possible to assess the reproductive output over the entire life span because *Capitella* sp. has a short life span and spawns repeatedly. *Capitella* sp. releases a limited number of eggs at each spawning, all of which are fertilized, allowing easy assessment of fecundity. Second, *Capitella* sp. with different developmental modes and habitats can be found in my study area, which provides a good comparison of how the environmental conditions affect the life history strategies of the animals. Third, the classification of the sibling species of *C. capitata* is mainly determined by electrophoretic analysis and by reproductive characteristics such as fecundity, egg size, and developmental mode. Although a large amount of variability in reproductive characteristics has been noted within each sibling species (Grassle and Grassle 1976, Grassle 1980), relatively little is known about how much of the variability is genetically derived versus how much is environmentally derived. Therefore, one of the important studies is to combine field studies of the life history characteristics of *Capitella* sp. with laboratory studies of how sibling individuals respond to different environmental factors (Grassle 1984). Fourth, *C. capitata* has been used as an indicator species of polluted marine areas for over thirty

years since its population density usually increases with intensifying organic pollution in a given area.

C. OBJECTIVES OF THE RESEARCH

In the present study, the emphasis has been placed on the effects of food quantity, food quality, the animal's age, and spawning sequences on reproductive characteristics. The last two factors will be considered together because they are closely related. The questions addressed in this thesis are: (1) Are the reproductive characteristics of different populations of *Capitella* statistically different? (2) Do the reproductive characteristics of sibling individuals differ in the field ? (3) Do the reproductive characteristics of *Capitella* vary with the spawning sequences ? (4) How does an animal's age affect its reproductive characteristics (e. g., fecundity, egg size, and egg energy content)? (5) How do the quantity and quality of food affect an animal's fecundity, egg size, egg energy content, and development mode? (6) Do animals with different developmental modes have similar responses to similar conditions of food quantity and quality? and (7) Do animals with different developmental modes have similar reproductive output or effort?

D. GENERAL ORGANIZATION OF THE THESIS

The central focus of this research is on the reproductive characteristics of *Capitella* sp. under different environmental conditions. This thesis, following the university guideline for "a paper format" of a Ph. D. dissertation, is divided into eight somewhat independent chapters and each chapter (except Chapters I and VIII) is organized as a manuscript for submission to journal. Thus, it is inevitable that some information, particularly in section of Materials and Methods, Discussion, Literature cited, is repeated a number of times.

Chapter II describes the population dynamics with special attention to recruitment. A new method I developed for marking and recapturing the animals in the field was

described; this method enables me to measure the growth, recruitment, and mortality of post-settled individuals, as well as fecundity, *in situ*. Chapter III describes the general reproductive characteristics of *Capitella* in the study area and the reproductive output and energy budget of animals with different developmental modes are quantified. Laboratory experiments were designed to allow assessment of the effects of aging on the fecundity, egg size, egg energy content, and total reproductive output of both lecithotrophic and planktotrophic developers by following the reproductive events of individual animals. In Chapter IV, I examine the effects of food quantity on reproductive characteristics by raising sibling individuals on different food rations. In Chapter V, I examine the effect of food quality on reproductive characteristics of two populations (both of which have planktotrophic development) that are considered to be subspecies by altering the food types given to sibling individuals derived from each population. In Chapter VI, I compare the effects of food quality on the reproductive characteristics of two populations of *Capitella*, one of which had lecithotrophic development and one of which had planktotrophic development, by providing sibling individuals of each developmental mode with four different kinds of sea plants. In Chapter VII, I study the "morphological females", obtained by rearing them from newly-settled juveniles in isolation, using histological and electron microscopic techniques to investigate the reproductive structures. Chapter VIII summarizes and discusses the various subjects present in Chapter II-VII.

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CHAPTER II

POPULATION DYNAMICS AND RECRUITMENT

A. INTRODUCTION

In a given area, the patterns of distribution and abundance of benthic marine invertebrates depend upon both the number of larvae (indirect developers) and juveniles (for asexual and direct developers) that can recruit into the habitat, and the number of these new recruits that survive to sexual maturity and finally reproduce (Thorson 1966, Chia 1989). Previous studies on recruitment and population dynamics of benthic marine invertebrates have focussed on intertidal epifauna that live on mudflats, rocks, algae, and other hard substrata (Crisp 1974, Scheltema 1974, 1986, Doyle 1975, Chia 1978, Barker 1979, Willams 1980, Grosberg 1981, 1982, Cameron and Rumrill 1982, Keough and Downes 1982, Young and Chia 1982, Dewolf 1983, Keough 1983, Ambrose 1984a, 1984b, Chia *et al.* 1984, Caffey 1985, Connell 1985, Gaines and Roughgarden 1985, Gaines *et al.* 1985, Gallagher et al. 1985, Hadfield 1986, Rumrill 1987, 1989, McShane *et al.* 1988, Rowley 1989). Most reports on recruitment and population dynamics of polychaetes have examined the relationship between population density and potential environmental factors such as quality and quantity of food, predation, and disturbances (Davis and Reish 1975, Tenore 1975, 1977, 1981, 1983, Warren 1977, Oliver 1979, Wilson 1980, 1981, Kent and Day 1983, Chesney and Tenore 1985, Oliver and Slattery 1985, Tamaki 1985, Tenore and Chesney 1985, Levin and Creed 1986, Beukema 1987). Only a few studies have successfully assessed the impact of post-settling mortality on recruitment of infaunal marine invertebrates (Commito 1982, Luckenbach 1984, Woodin 1985, Watzin 1986). Field experiments dealing with settlement and recruitment of infauna have proven difficult because one must time the experiments exactly with the peak of settlement for the designated species, find an appropriate method to sample newly-settled juveniles, measure the differential mortality of post-settling stages, and measure growth

rate and reproduction. As far as I know, there are only 5 such field experimental studies (Williams 1980, Levin 1981, Gallagher *et al.* 1983, Luckenbach 1984, Woodin 1985).

The polychaete worm *Capitella capitata* has become well known among ecologists as a marine pollution indicator species. More recently, studies of *C. capitata* have been directed toward describing its sibling species on the basis of differences in reproduction, life-cycles, and population growth (Grassle and Grassle 1974, 1976, 1977, 1978, Grassle 1980). Previous population studies of *Capitella* (Tenore 1975, 1977, 1981, 1983, Warren 1977, Tenore and Chesney 1985, Wu et *al.* 1988, Grémare *et al.* 1988, 1989a, 1989b) have failed to integrate the events of the spawning cycle, larval abundance, larval growth, settlement, differential mortality and growth of post-settling stages, and fecundity.

In this study, both laboratory and field experiments were conducted to examine factors that may affect the recruitment and population dynamics of *Capitella*. These factors include the reproductive cycle of an established population, the abundance and distribution of larvae in the plankton, the proportion of juveniles in the population, the size-dependent mortality of juveniles and adults, the growth rate of juveniles and adults, the fecundity of adults, predation upon pelagic larvae by pelagic predators, benthic predation upon settling larvae or juveniles, net recruitment, and the effect of seaweed mats on recruitment.

B. MATERIALS AND METHODS

In Barkley Sound, British Columbia, Canada, *Capitella* sp. can be found in protected intertidal and subtidal soft bottom habitats. A small population, located in the intertidal mudflat in Grappler Inlet, was chosen for this study because of its accessibility. Here, *Capitella* is associated with other polychaetes such as *Glycera* spp., *Lumbrineris zonata*, *Dorvillea japonica*, *Paraonella spinifere*, and *Polydora ligni*. Other representative members of this soft-sediment community include the green algae, *Enteromorpha* and

Ulva spp. (in the spring and summer); the eelgrass, *Zostera marina*, and the opisthobranch *Haminoea velicula*. *Polydora ligni* is the major predator species on the settling larvae and juveniles of *Capitella*, while *Glycera* spp. and *Nereis* spp. are the major infaunal predators on adult *Capitella*.

1. Study site

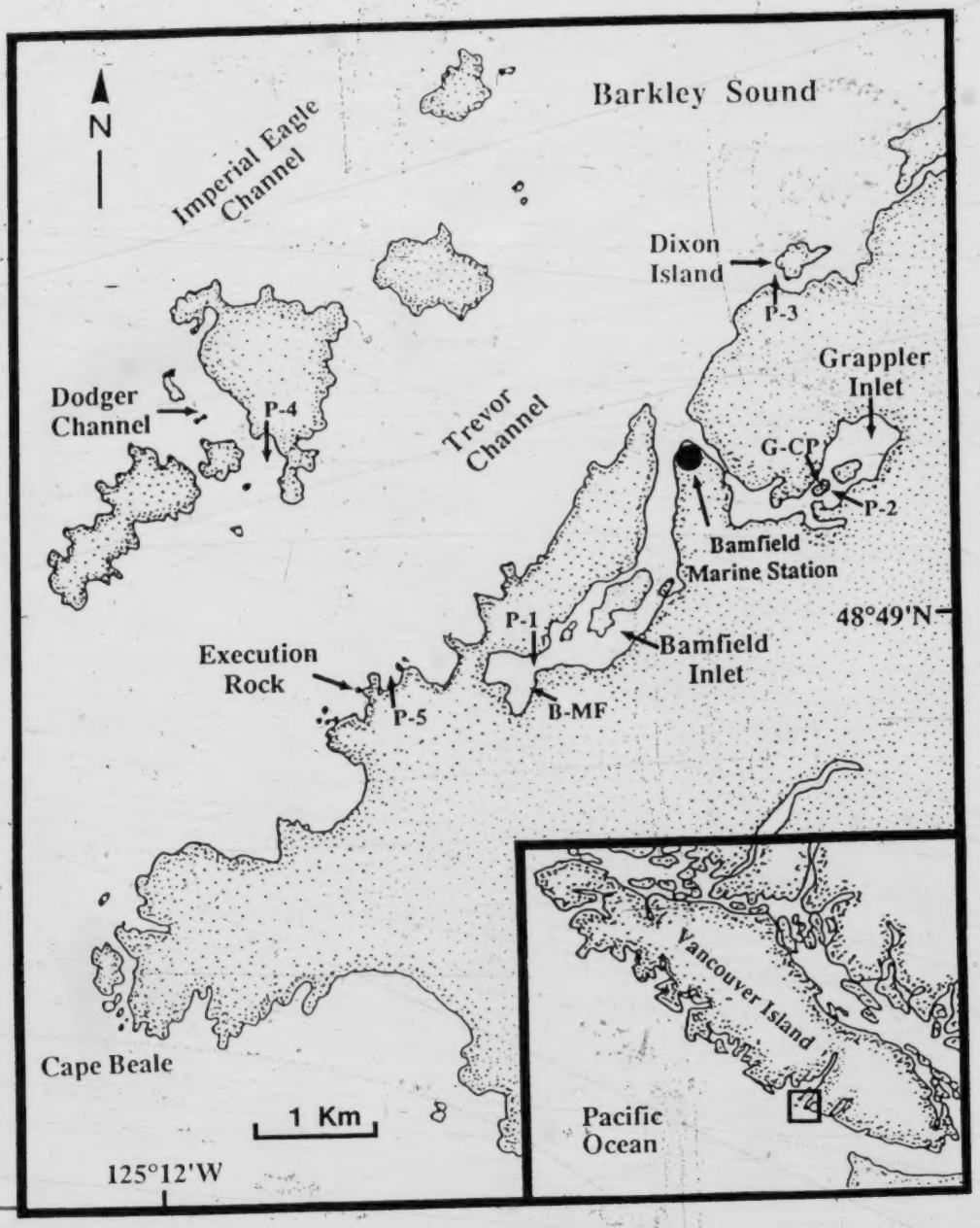
The study was conducted from May 1986 to August 1988 in the vicinity of the Bamfield Marine Station, British Columbia, Canada (48°50'N, 125°08') (Fig. II-1). Grappler Inlet is an estuarine tidal channel that extends inland for about 2 km. Tides in this inlet are mixed and semi-diurnal with a vertical range of 3.6 m. The study site was located on a small island near the head of the inlet (Fig. II-1). Ninety-four per cent of the sediment particles at the study site were smaller than 0.06-0.004mm (silt). The degree of exposure to ocean swells and wave surge was also the lowest in this area (Rumrill 1987)

The deposition rate of detritus in the study site was assessed by placing 4 jars (with a 10 cm diameter opening) in the mid-intertidal region at this site. Jars were brought back to the laboratory and all detritus in each jar was emptied into pre-weighed aluminum pans and dried in an oven at 100°C for 12 h to obtain the dry weight. Organic material was removed from the detritus by placing it in an oven 425°C for 4 hours. The amount of organic material in the detritus was calculated by subtracting dry weight of the remaining ash from total dry weight of detritus.

2. Abundance

Between February 1987 and April 1988, the abundance and size-frequency distributions of *Capitella* at the Grappler Inlet site were estimated by sampling quadrats (5x5 cm^2) at 3 points along each of three 15 m transects; the transects were chosen to correspond with the high, middle, and low intertidal levels. All samples were washed gently with a sieve (mesh size: 200 μm) in the laboratory. *Capitella* and other polychaetes were retained, counted, and expressed as the number of worms per m^2. Size-frequency

Figure II-1: Location of the sampling sites for *Capitella* sp. in Barkley Sound, Vancouver Island, British Columbia. P_1-P_5 indicate 5 plankton sampling sites; B-MF indicate the mudflat in Bamfield Inlet where the experimental trays and cages were placed; G-CP indicates the location of intertidal population of *Capitella* sp. in Grappler Inlet where benthic samples were collected monthly and where the growth, mortality and fecundity of marked sibling *Capitella* were measured *in situ*. Map was modified from Roland (1980).


N
Barkley Sound
Imperial Eagle Channel
Dixon Island
P-3
Grappler Inlet
Dodger Channel
P-4
Trevor Channel
G-CP
P-2
Bamfield Marine Station
48°49'N
P-1
Bamfield Inlet
Execution Rock
P-5
B-MF
Vancouver Island
Cape Beale
1 Km
Pacific Ocean
125°12'W

data were obtained by measuring the body length, body diameter and body volume of each unbroken individual in the samples.

3. Reproductive cycle

The reproductive cycle of *Capitella* was determined by estimating the relative proportion of six different reproductive stages in each month sample: 1. juveniles, 2. young adults that show barely visible ovaries, 3. adults that have well-developed ovaries but have no eggs in their coeloms, 4.adults that have eggs in their coeloms, 5. adults that have their coeloms packed with eggs and are ready to spawn, and 6. adults that have just spawned (Wu and Qian 1988). Males, females, and hermaphrodites were distinguished by visible gonads or/and copulating spines.

4. Larval abundance and distribution

Polychaete larvae in the plankton were sampled every 2-4 weeks between May 1986 and June 1988. Samples were collected at five sites -- three were coastal sites [at the head of Bamfield Inlet (P-1), in Grappler Inlet (P-2), and near Dixon Island (P-3)], while two were in two more exposed waters [Execution Rock (P-4) and Dodger Channel (P-5)] (Fig. II-1). Samples were collected from a depth range of 2-3 m using a standard plankton net (125 μm). Sampling was standardized as closely as possible by timing each tow 2 to 3 hours before the daytime high tide. Tows were carried out for 5-10 minutes from a 4-meter vessel moving at about 2 knots. The net was kept at a depth range of 2-3 m using a buoy and a buck of lead attached to the opening of the plankton net. The amount of water passed though the net was calculated using an "Oceanic" flow meter which was positioned at the opening of the net.

Plankton samples were brought to the laboratory immediately after collection and, with a few exceptions, the majority were sorted live. All sorting was carried out in a Bogorov Tray. When sorting became difficult during the spring and fall blooms, samples were divided into eighths, quarters, or halves with a plankton separator. For each sample, the total number of polychaete larvae was determined. All larvae were identified to family

or species on the basis of morphology and pigmentation. The larvae of each species were counted under the dissecting scope. The larval abundance of *Capitella* in the plankton was followed throughout two years.

5. Larval settlement

In the laboratory, mud collected from different habitats was given to competent larvae to test their preference of settlement. There were six treatments, including controls (no mud) and mud from the head of Bamfield Inlet, Execution Rock, Brady's Beach, the head of Grappler Inlet, and adult habitats in Grappler Inlet. Three replicates, each containing thirty larvae, were used for each treatment. Larvae were reared in 60 ml culture beakers and fed a mixture of ground *Ulva* and phytoplankton concentrated from natural seawater. The cultures were maintained in an incubator at 10-11°C and seawater was changed daily. The number of settled juveniles was recorded every day.

6. *In situ* measurement of mortality, recruitment, growth, and fecundity

a. Neutral red solution: 500 mg of neutral red (Fisher Scientific Company, total dye content 54%) were added to 100 ml of 0.45 µm filtered seawater and stirred gently. Insoluble materials were then filtered out with 25 µm mesh. This solution was used as the stock and was stored under dark, cold conditions.

b. Staining procedure

The larvae and embryos used for the experiments were added to small Petri dishes (3.5 cm in diameter) containing 3-4 ml of filtered seawater (0.45 µm). Two or three drops of the neutral red stock solution were then added to the seawater. Animals were stained for 2 minutes prior to being transferred to a Petri dish containing filtered seawater. Here, larvae were washed twice. Juveniles used for the field experiments were stained slightly longer and the duration of staining was dependent on the animal's size.

c. Effect of staining on survival and development

Fertilized eggs, young embryos, and larvae of *Capitella* sp. and 3-setiger larvae of *Nereis vexillosa* were obtained through laboratory culture. The larvae of *Polydora ligni*, *Spirorbis* sp., and *Polynoid* sp. were collected from plankton. Twenty-five to one hundred stained larvae were reared in 1 liter culture beakers or in culture trays (5x5 x5 cm) with running seawater at 10±1°C. Larvae were fed with a mixture of *Isochrysis qualbanam, Monochrysis lutheri, Phaeodactylum tricornutum*, and ground *Ulva*. The mortality of stained larvae was compared with that of the unstained siblings of each species (control groups). The larval mortality, growth rate, juvenile mortality, and fecundity of *Capitella* were compared. The growth of *Polydora ligni* larvae was also compared. For most comparisons, the experiment was run with 3 replicates.

d. Mortality, growth, and fecundity measured *in situ*

The mortality, growth, and fecundity of *in situ Capitella* were determined directly by raising stained (marked) and newly-settled sibling juveniles in trays (15x15x15 cm) placed in the mid-intertidal zone at the Grappler Inlet study site. Each tray contained a 12 cm layer of mud substratum that was collected and sieved *in situ* through a 200 μm mesh sieve to exclude potential predators and competitors. The trays were brought back to the laboratory every 2-3 weeks, and all marked animals were recovered from each tray. To determine the mortality of animals of different size (ages) classes, the number of marked animals alive at the beginning and end of each interval was counted and compared. To determine the growth rate, the mean body size and mean number of setigers of more than 30 individuals were measured at the beginning and the end of each interval. Prior to measurement, the animals were relaxed in 0.36 M $MgCl_2$ and then measured with the aid of a microscope equipped with a micrometer. Undamaged animals were selected and returned to trays, and the experiments were continued until animals released eggs in their tubes. To determine the fecundity (number of eggs per spawn) in the field under these defined environmental conditions (without predation pressure and at low density), the

newly-shed eggs in the tube of each spent animal developed from marked juveniles were counted under a dissecting microscope.

e. *In situ* recording of recruitment

In order to determine the recruitment rate of *Capitella* into the intertidal mudflats, 12 trays (15x15x15 cm) were placed in the mid-intertidal zone. The opening of each tray was 2 cm above the surface of the substratum. Each tray contained a 12 cm layer of sand collected in the manner described above. All trays were left in the field for 2-3 weeks before being brought back to the laboratory. In the laboratory, mud in each tray was sieved through a 200 μm mesh sieve. The number of *Capitella* juveniles and other polychaetes was counted under a dissecting microscope. The body size of *Capitella* juveniles was measured using the methods described in Section 6.

7. The effect of drifting seaweed on mortality and recruitment

In order to determine the effect of drifting seaweed on mortality and recruitment, a rectangular cage made of 0.8 cm mesh galvanized hardware cloth was anchored on top of each of six trays. The structure prevented seaweed from falling into each tray. Another six trays that were left uncovered were used as controls. The mortality of marked juveniles in the treatments was compared with that of controls after 3 weeks. The number of newly-settled juveniles in the treatments and controls was also compared to examine the effect of drifting seaweed on recruitment. This experiment was only conducted for three successive months in the summer of 1988 because of the considerable time required to sort through such a large quantity of sand.

8. Laboratory experiments on predation

a. Predation upon pelagic larvae by pelagic predators

The first stage zoeae of *Hemigrapsus oregonensis*, zoeae of *Petrolisthes eriomerus*, and newly-hatched squid (*Loligo* sp.) were used as predators. Predators were starved for 12-24 hours prior to the experiments; feeding experiments were conducted for 24 hours with a 8D/16L photoperiod on slowly rotating grazing wheels kept at 12±1°C.

The predators and prey were suspended in 1 liter jars that contained 1 liter of filtered seawater (1μm filter) (Rumrill 1987).

Newly-hatched trochophores of *Capitella* were used as prey to examine the density-dependent characteristics of predation by the three species of predators. The experiments consisted of four replicates at five prey densities: 25, 50,100, 200, and 400 individuals per jar, as well as duplicate controls. After 24 hours, the number of prey remaining in each jar was counted.

Clearance rates were calculated using the following equation:

$$N_t = N_0 e^{-mt}$$

$$F = Vm/P$$

where **F** is the clearance rate in liters per predator per day, **m** is the instantaneous prey mortality rate per day, N_0 is the initial number of prey per jar, N_t is the final number of prey per jar, **P** is the number of predators per jar, **t** is the duration of the experiment in days, and **V** is the volume of the experimental jars (Greene 1986).

When calculating the clearance rate, the mean number of prey remaining in the controls for each type of prey, at each density, was used as the new N_0; this took into account the loss of prey due to transfer procedures. A two-way ANOVA was calculated for all predators and all prey densities to check for predator effects and density effects.

b. Predation upon competent larvae, settling larvae, and post-settling juveniles by benthic predator.

Aquaria (5x5x5 cm) inhabited by two *Polydora ligni* predators were used as experimental chambers. Newly-hatched trochophores, competent larvae, settling larvae, and post-settling juveniles of *Capitella* sp. were used as prey. Each aquarium (with a 35 μm mesh wall) was provided with running seawater and set in a shallow seawater table at 10±1°C. For each type of prey, the experiments were conducted at densities of 25, 50, 100, 200, and 400 prey per aquarium. Each treatment consisted of four replicates (with predators) and 2 controls (without predators). The number of larvae or juveniles captured

was determined by subtracting the number of survivors recovered at the end of the experiment from the initial number of prey. All experiments were conducted for 24 hours.

C. Handling times of the predator on different prey

A beaker inhabited by one *P. ligni* was placed under a dissecting microscope. Trochophores, competent larvae, and post-settling juveniles of *Capitella* were added to the beaker. The time each predator spent between making a successful encounter with a prey to ingesting that prey was measured with a stopwatch. For each type of prey, the predator's handling time was recorded 20 or more times. The swimming speed of the prey was also measured in a small aquarium by measuring the time larvae took to cover a certain distance.

All statistical analyses were carried out following the methods outlined by Zar (1984) and Sokal and Rohlf (1981).

C. RESULTS

1. The polychaete community and some environmental parameters at the study site

The habitat occupied by *Capitella* in a area of about 70 m^2 at the Grappler Inlet study site also contained sympatric polychaete species such as *Lumbrineris zonata, Dorvillea japonica, Paraonella spinifera, Glycinde picta, Polydora ligni, Nereis* spp., and *Polynoid* spp. In the spring and summer, the green algae *Ulva lactuca* and *Enteromorpha* provided these worms with varying food sources. In fall and winter, rotted *Zostera marina*, kelp (mainly *Macroscytis* and *Nereocystis*), and other detritus served as the main food source for *Capitella*. At the study site, detritus deposited at an average rate of 310.5 ± 55.5 g/day/m^2 (8 replicates) which contained 40.5 ± 0.81 g organic material/day/ m^2. The highest polychaete density (about 11500 ind/m^2) occurred in July 1987. The polychaete density not only showed distinct seasonal changes

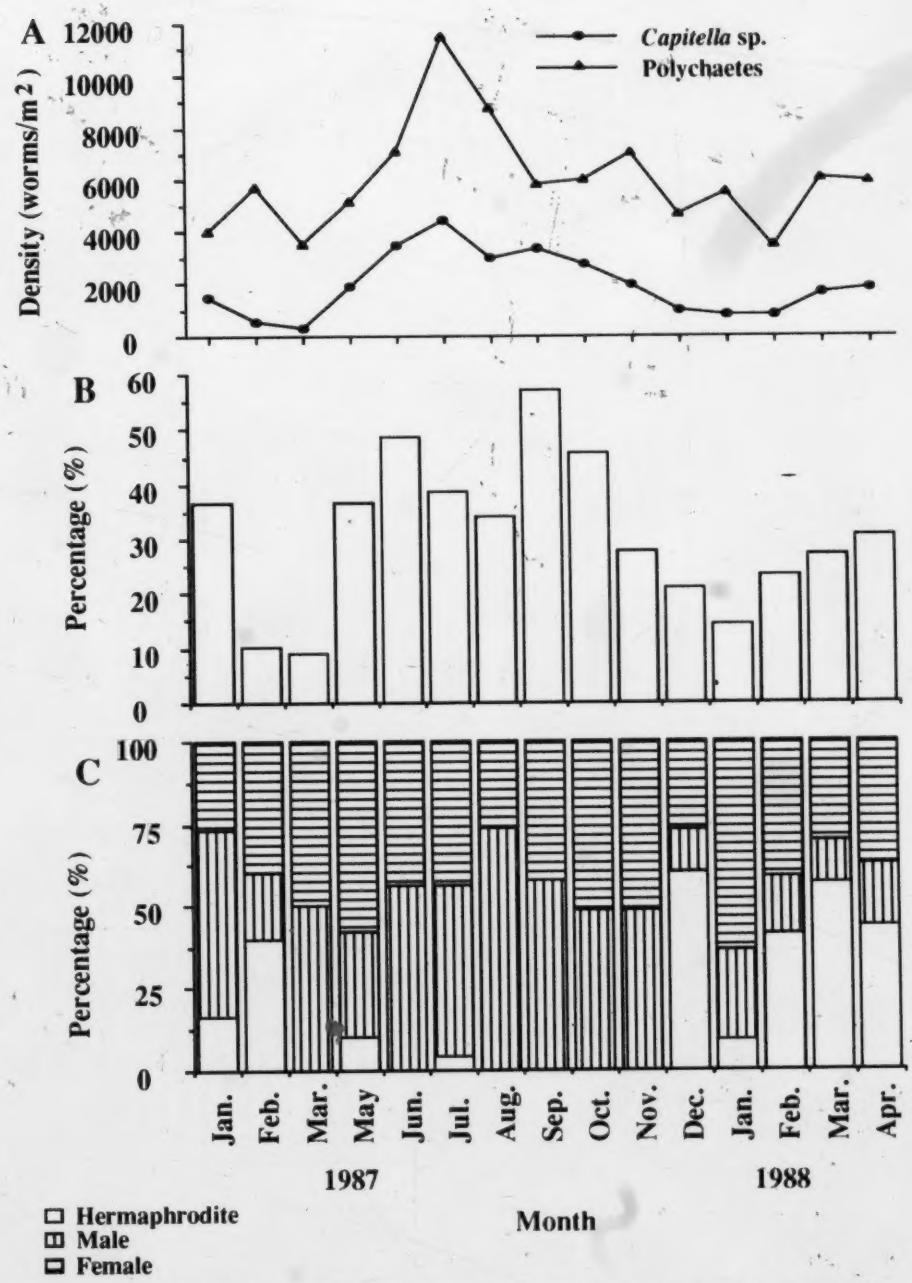


Figure II-2: Population density of *Capitella* sp. at the Grappler Inlet study site: A, *Capitella* sp. abundances and polychaete density; B, *Capitella* sp. relative abundance in benthic polychaete community (12 species); C, proportions of hermaphrodites, males, and females of *Capitella* sp.

(Fig. II-2A) but also showed a different distributional pattern at different tidal levels (Kruskal-Wallis, H=10.28, P<0.01).

Ambient seawater temperatures (surface) in the study area varied seasonally; the highest temperature occurred in the summer months and the lowest in January (Fig. II-3). However, the interstitial seawater temperatures at the Grappler Inlet study study site varied even in a larger ranges (from -1°C in January to 17°C in June), unfortunately, I was able to monitor the seasonal changes closely. NO_3 concentration in seawater also varied seasonally from 0.13-13.86 μM/liter for surface seawater and 5.9-25.3 μM for the seawater in the seawater system of the Bamfield Marine Station (the water was pumped from Bamfield Inlet at a depth of over 18 meters) (Fig. II-4A and 4B). NH_4 concentration in the seawater varied from 0.34-4.7 μM for surface seawater and from 0.6-5.9 μM for the seawater in the seawater system of the Bamfield Marine Station (Fig. II-5A and 5B).

2. Population density

Although the population density and distribution of *Capitella* fluctuated over the sampling period, there appeared to be clear trends. First, changes in the abundance of *Capitella* sp. and polychaetes in the study area showed a similar pattern (Fig. II-2A, Kendall's test: r=0.584, P<0.01); the proportion of *Capitella* in the total polychaete biomass varied with the season (Fig. II-2B). In September 1987, *Capitella* consisted of 57% of the total polychaete biomass, which was much higher than the average proportion of *Capitella* in the polychaete biomass (30%). Second, the highest population density (4445 worms/m^2) occurred in summer, but in winter or early spring, the population density declined considerably (lower than 300 worms/m^2). Third, the distribution of *Capitella* and other polychaetes at the sampling site was affected by intertidal levels (Kruskal-Wallis test, *Capitella*: H=7.35, P<0.05; polychaete biomass: H=8.42, P<0.05). Surveys indicated that a large proportion of these animals are distributed in the high- to mid-tide regions of the intertidal zone, and that the highest density was found in the mid

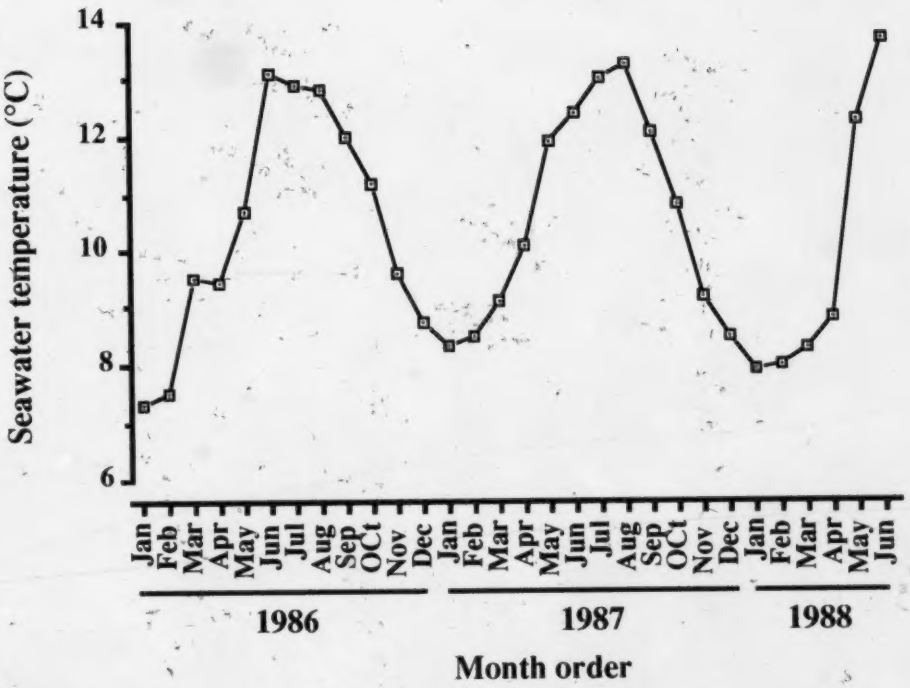


Figure II-3: Seasonal variations in surface seawater temperature at Cape Beale, near the Bamfield Marine Station. Values plotted are the monthly averaged temperature. Data were Provided by P. Janitis.

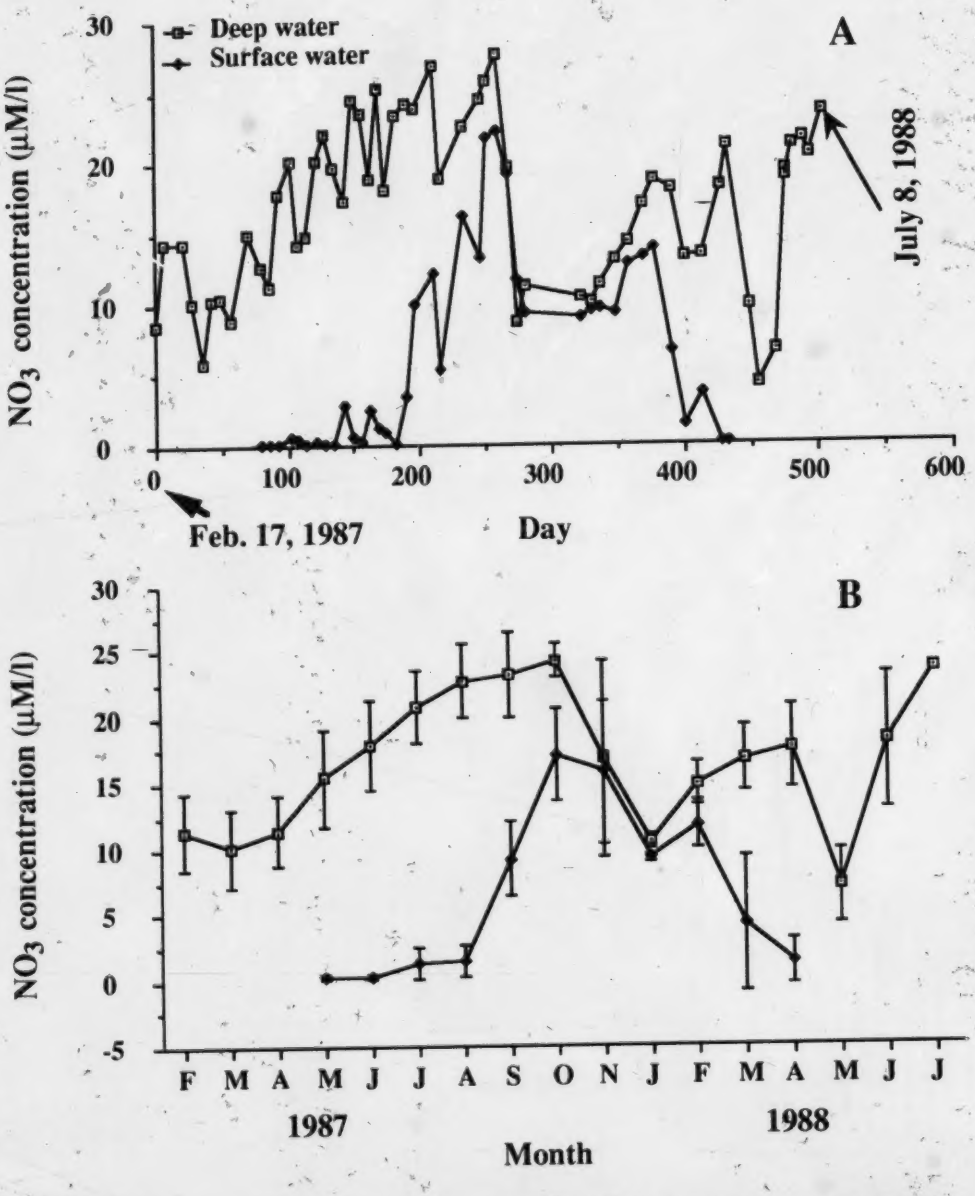


Figure II-4: Seasonal cycle of NO_3 concentration (μM/l) in the seawater system of Bamfield Marine Station (pumped from about 18 m deep in Bamfield Inlet) and in seawater collected from sea surface of Bamfield Inlet. A, NO_3 concentration changes in two years; B, monthly averaged NO_3 concentrations. Data were provided by L. Rimmer.

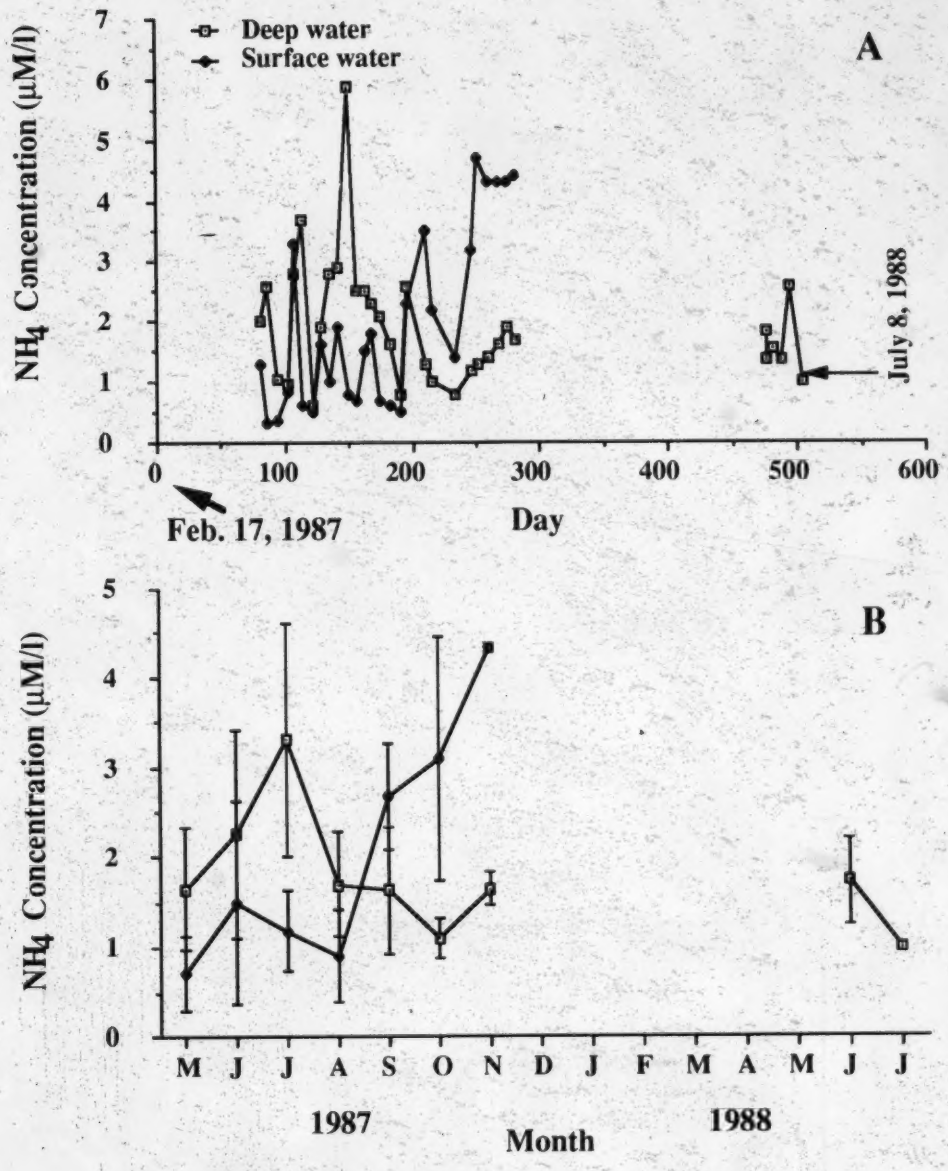


Figure II-5: Seasonal cycle of NH_4 concentration (μM/l) in the seawater system of the Bamfield Marine Station (pumped from about 18 m depth in Bamfield Inlet) and in seawater collected from sea surface of Bamfield Inlet. A, NH_4 concentration changes over two years; B, monthly averaged NH_4 concentration. Data were provided by L. Rimmer.

intertidal zone in July 1987. In addition, the proportion of males, females, and hermaphrodites varied seasonally (Fig. II-2C).

The size frequency distribution of *Capitella* revealed that the population (Fig.II-6) contained a high proportion of new recruits in summer. Animals in most samples fell into two distinct cohorts based on body size, that is, a juvenile cohort (< 12-14 mm in body length) and an adult cohort. Growth rate data suggested that animals with a body length of 2-6 mm were about 1 month old and animals with a body length of 6-14 mm were about 1.5-2 months old.

3. Reproductive activity

The presence of juveniles year-round indicated that this population was reproductively active throughout the year. The reproductive cycle was characterized by a higher percentage of juveniles and young adults in summer (Fig. II-7). Another striking characteristic was the high percentage of pre- and post-spawning individuals appearing in winter and early spring, which was correlated with a small peak in larval abundance in the plankton.

4. Larval abundance, distribution, and settlement

Kendall's coefficient of rank correlation tests revealed similar patterns in the abundance of polychaete larvae in the three protected areas (Table II-1). However, there was a difference between the protected area and the exposed area. The abundance of polychaete larvae in the protected water was much higher than in the exposed areas. The distribution and abundance of *Capitella* larvae showed similar trends. A very high density of *Capitella* larvae has been recorded in three protected areas, but *Capitella* larvae were rarely found in the plankton from Dodger Channel or Execution Rock. The abundance of larval polychaetes and *Capitella* in Bamfield Inlet was about one order of magnitude higher than in Grappler Inlet and Dixon Island, and two to three orders of magnitude higher than in Dodger Channel and Execution Rock (Fig. II-8A, B, C, and D). The larval density of all polychaetes and *Capitella* tended to increase to a peak in early

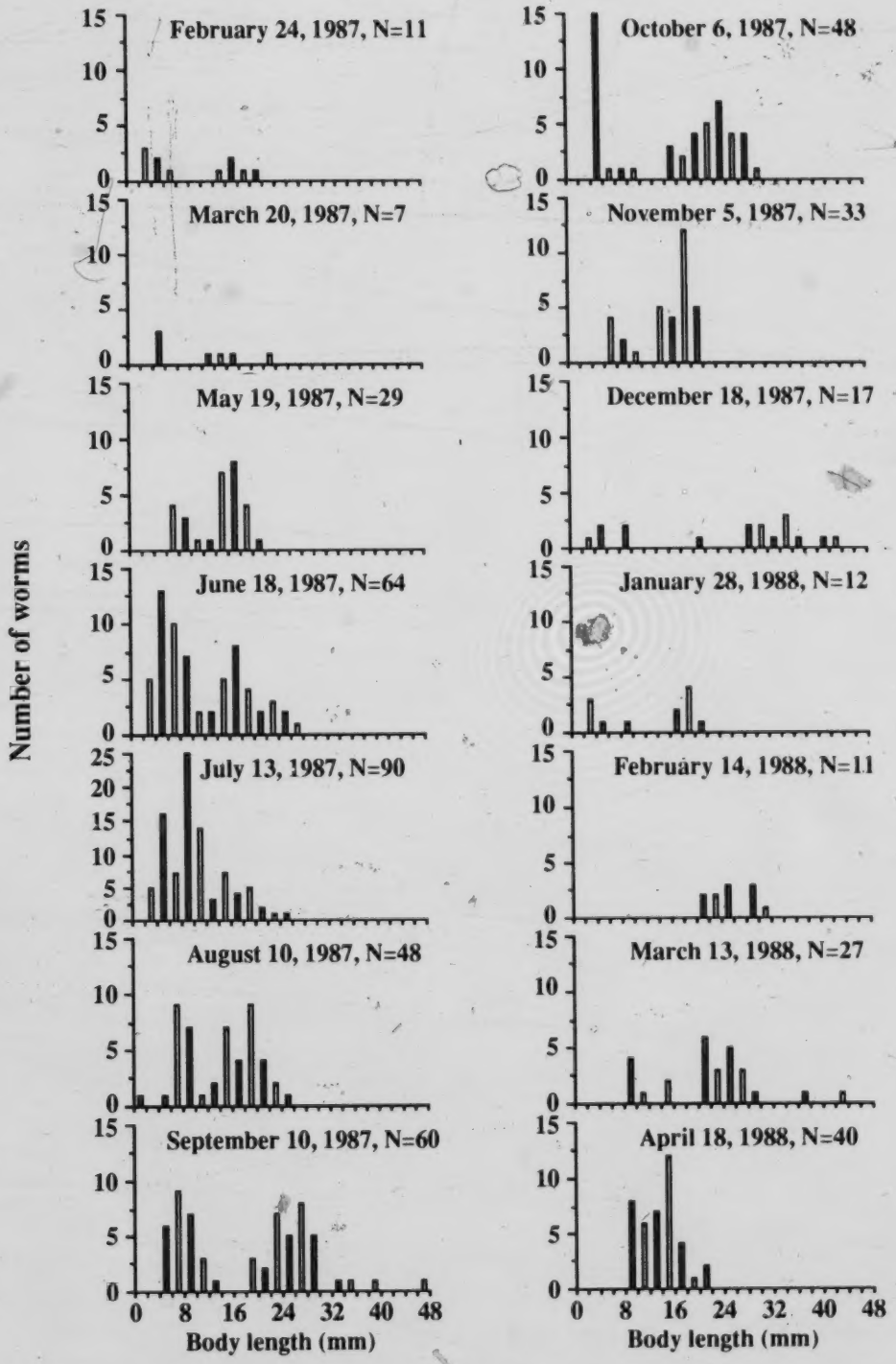


Figure II-6: Size frequency distribution of *Capitella* sp. at the Grappler Inlet study site.

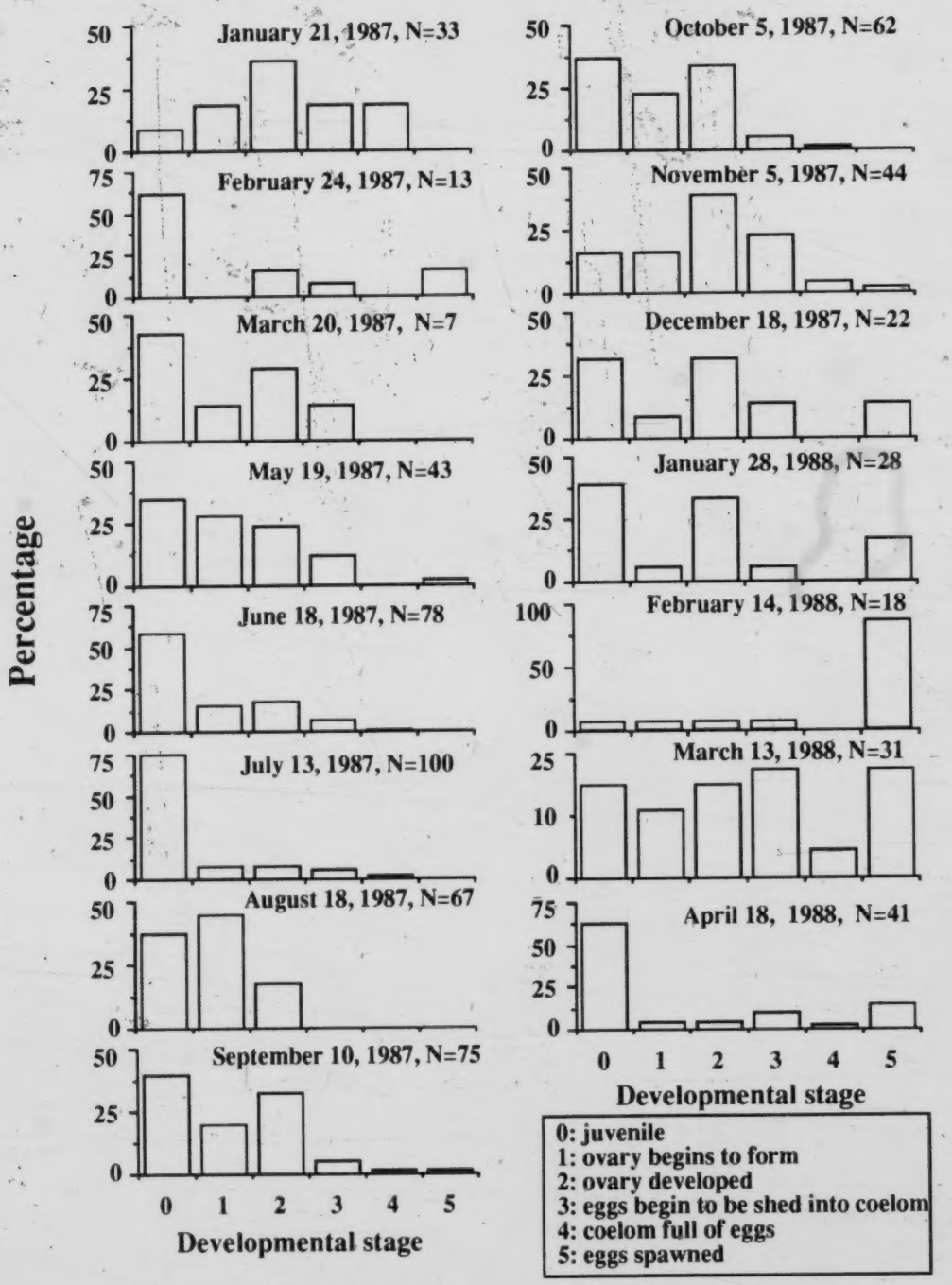


Figure II-7: Frequence distribution of six reproductive stages of *Capitella* sp. at the Grappler Inlet study site. The developmental stages are defined arbitrarily as above.

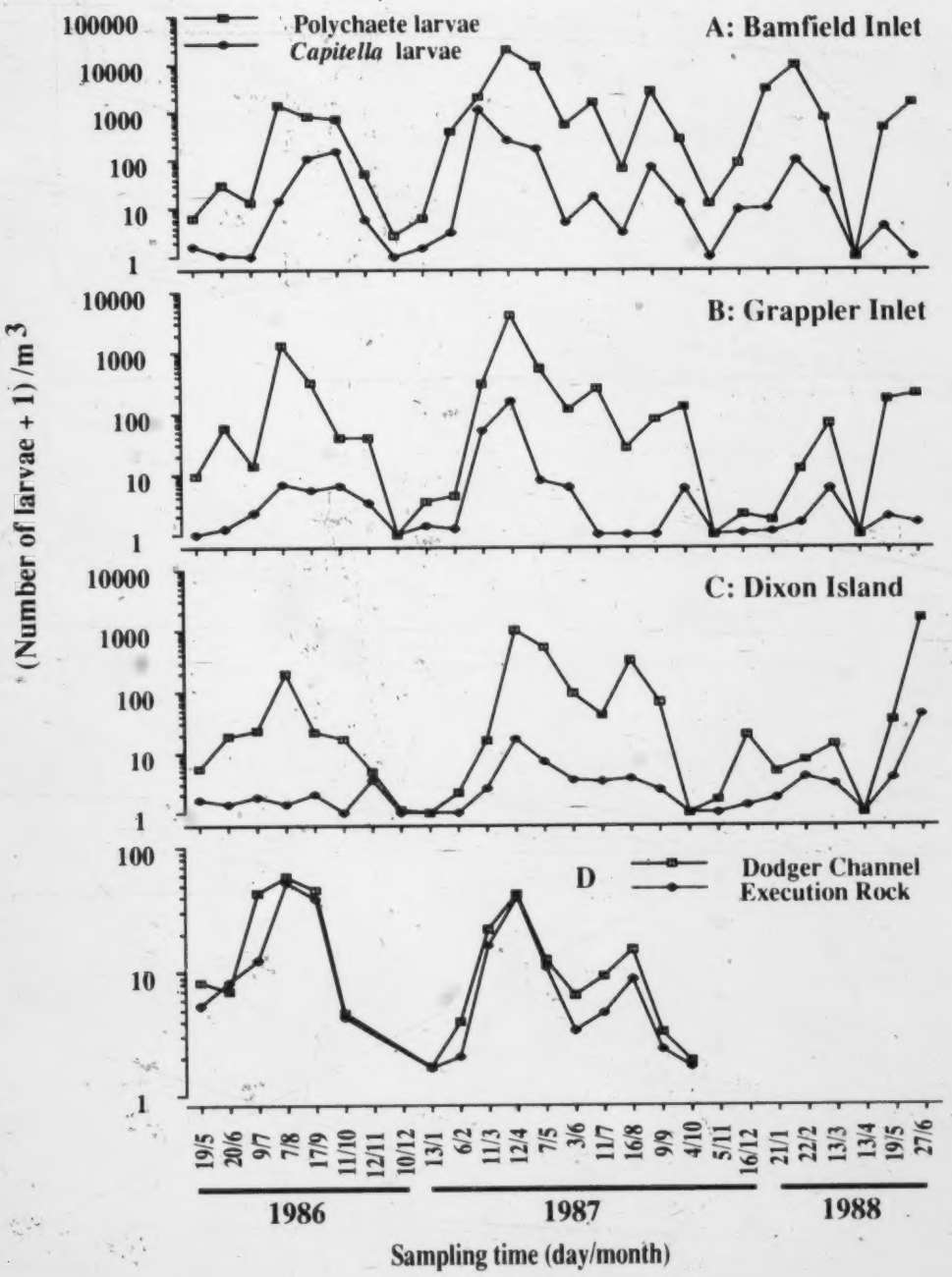


Figure II-8: Seasonal changes in densities of polychaete larvae and *Capitella* sp. larvae at five sampling sites in the Barkley Sound. A, Bamfield Inlet; B, Grappler Inlet; C, Dixon Island; and D, polychaete larvae from Dodger Channel and Execution Rock.

Table II-1: Kendall's coefficient of rank correlation test: abundance of polychaete larvae and *Capitella* sp. larvae at the five sampling sites.

Sampling sites(A vs. B)	Pairs	t	P
Total polychaete larvae			
Bamfield : Grappler	26	0.619	0.001
Bamfield : Dixon	26	0.483	0.012
Bamfield : Dodger	16	0.048	0.44
Grappler : Dixon	26	0.578	0.002
Grappler : Dodger	16	0.048	0.44
Dixon : Dodger	16	0.048	0.44
***Capitella* larvae**			
Bamfield : Grappler	26	0.521	0.500
Bamfield : Dixon	26	0.307	0.017
Grappler : Dixon	26	0.267	0.034

spring, declined in early summer, but increased again to a second lower peak in early fall at the three protected sites. This pattern appeared to match the seasonal changes of nutrient concentration or temperature changes in the water system, and also appeared to match the seasonal changes of phytoplankton concentration in this region (personal observations).

In the laboratory experiments, larvae showed no preference for substratum (mud) collected from any of the sites; they settled equally well in the control (no mud) (ANOVA test: $P>0.05$) during a period of 4-day experiments.

5. The effect of staining (dye) on larval survival, growth, and reproduction.

Table II-2 summarizes the results of the effects of neutral red staining on the mortality, growth, and reproduction of 300 stained competent larvae of *Capitella* . These results indicated that neutral red had no effects on either larval settlement or post-settling stages or the fecundity of these animal. Moreover, Table II-3 lists the experimental results for the young trochophores and embryos of *Capitella* and the larvae of other 4 species. These results indicated that neutral red staining had no significant effect on larval mortality and development. Stained and unstained larvae and embryos of these species had similar survival rates and grew equally well.

6. *In situ* measurement of mortality, recruitment, growth, and fecundity

a. Growth

The body length, diameter, volume, and the number of setigers of siblings of four cohorts increased over the experimental time within the first 11 weeks (Fig. II-9 A - D). Also, the growth rate [in terms of daily increase of body volume (mm^3/day)] was significantly correlated with the animal's initial size (Fig. II-10 A). Specific growth rate of body-volume was inversely related to the initial size of juveniles and young adults (Fig. II-10 B). In other words, smaller animals had higher growth rates in terms of increase of

Table II-2: Effects of neutral red staining on survival, development, and fecundity of *Capitella* sp. with the results of Mann-Whitney Test at 0.05 level. Values are mean ± standard deviation (sample size).

	Control	Treatment	U value	P
Competent larvae(Feb. 24)	50±0 (3)	50±0 (3)		
Settling juveniles(Mar. 2)	27.7±7.6 (3)	30.7±8.5 (3)	5.50	0.42
Juveniles (Mar. 23)	20±4.6 (3)	22.7±6.5 (3)	5.5	0.42
Adult (May 10,1987)	11±3.0 (3)	11±1.7 (3)	5.0	0.44
Fecundity(eggs/spawn)	4932±1723 (9)	6582±1929 (6)	14.0	0.43

Table II-3: Effects of neutral red staining on larval survival and growth over 72 hours with the results of Mann-Whitney Test at 0.05 level. x experiments were conducted for 24 hours. Values are mean ± standard deviation.

Larvae or embryos	Control	Treatment	N	U value	P
	Survival rate				
Polydora ligni (3-setigers)	51.2%±4.6%	55.2%±11.2%	5	14.0	0.472
Polynoid sp.	65.0%±18.9%	61.9%±15.7%	3	5.0	0.462
Nereis vexillosa (3-setigers)	94.4%±1.9%	96.0%±4.0%	3	0.0	0.193
Spirorbis sp.	76.1%±4.5%	77.8%±6.0%	3	4.0	0.462
Embryos of *Capitella*x	83.9%±2.8%	85.4%±10.2%	4	10.0	0.434
Larvae of *Capitella*x	91.0%±6.9%	91.2%±6.8%	7	24.0	0.497
	Larval growth				
Length (mm) of *P. ligni*	1.35±11.8	1.35±7.7	25	305.5	0.499
Setigers of *Polydora ligni*	17.2±0.8	17.0±0.7	25	347.5	0.493

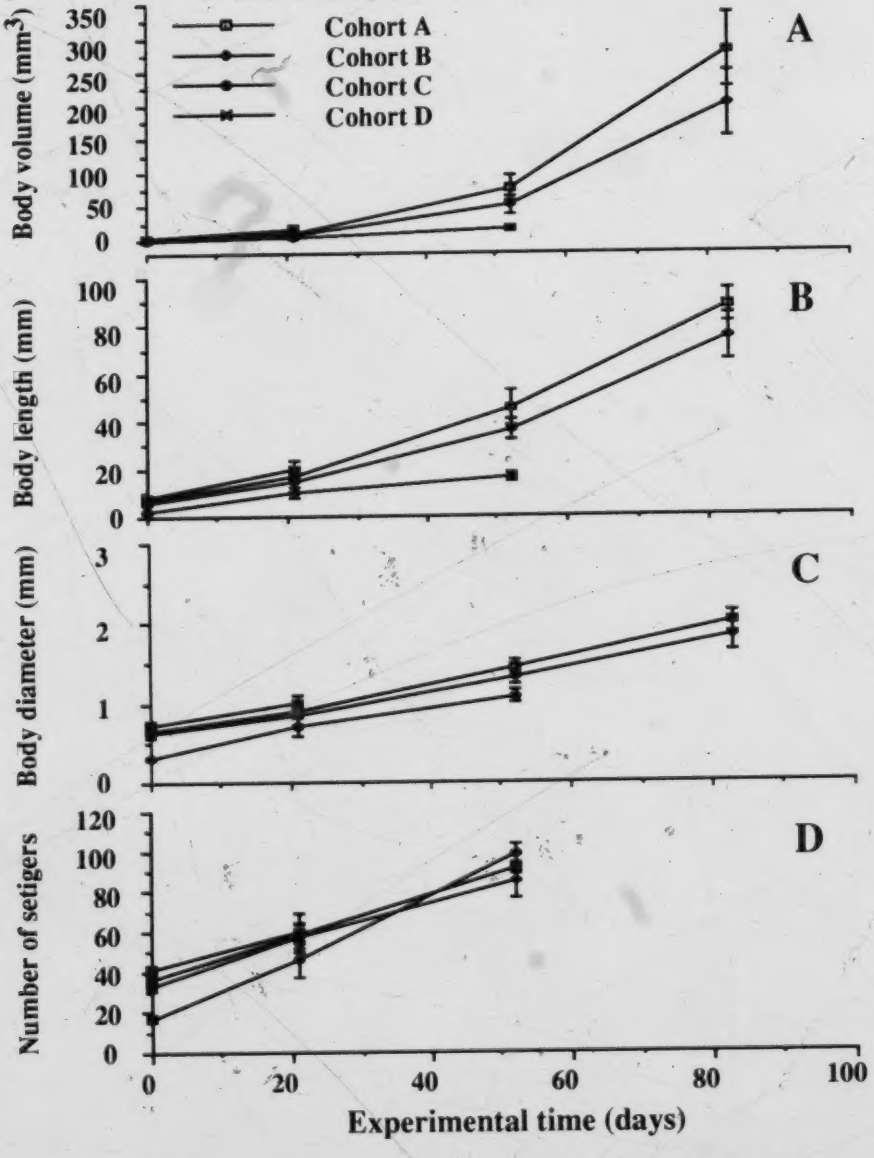


Figure II-9: Growth of *Capitella* sp. measured in the controlled experiments at the Grappler Inlet study site. Cohorts A-D represent the sibling juveniles from 4 different spawns. Data plotted are mean ± standard deviation of 30 animals measured for each point.

body volume. For instance, the increase in the body size of newly-settled juveniles (cohort C) was 8.5% of animal's size per day. Once animals began to develop gametes the growth rate decreased, although animals continued growing until spawning. The body size of a spent animal was smaller compared with its pre-spawning stage, but the loss was recovered gradually when plenty of food was provided. The growth rate of animals in the field was very similar to that of animals fed ground *Ulva lactuca*. in the laboratory (See Chapters V and VI).

b. Mortality

The mortality of *Capitella* under controlled conditions (without predation or competition) was affected by the size of animals (Kruskal-Wallis test: $H=17.6$, $P=0.014<0.05$). Figure II-11 shows that there was an exponential relationship between animal size and mortality. Young juveniles had a much higher mortality than adults. However, once animals reached a certain size (about 10 mm^3 of body volume) the survival rate became very high. The mortality of *Capitella* juveniles and young adults appeared to be mainly due to physical disturbance or emigration (Section 7). It is possible that many juveniles and young adults in the trays were washed away by intertidal waves while they attached to drifting seaweed or small cobbles.

c. Recruitment

Intense recruitment occurred in trays placed in the mid-intertidal zone at the Grappler Inlet study site during the summer of 1988 (Table II-4). Recruitment rates were significantly affected by the sampling time (Kruskal-Wallis ANOVA, $H=9.09$, $P=0.028<0.05$). Intense recruitment also occurred in the mudflat at the head of Bamfield inlet, although there was no distinct population of *Capitella* sp. found (Table II-4); from May 10 to June 7, 1988, there were 917±520 *Capitella* juveniles/m^2 (6 replicate trays) found in the trays; the daily averaged recruiting rate was 30.6 worms/m^2/day, which was lower than that in Grappler Inlet (56 worms/m^2/day) during the same period.

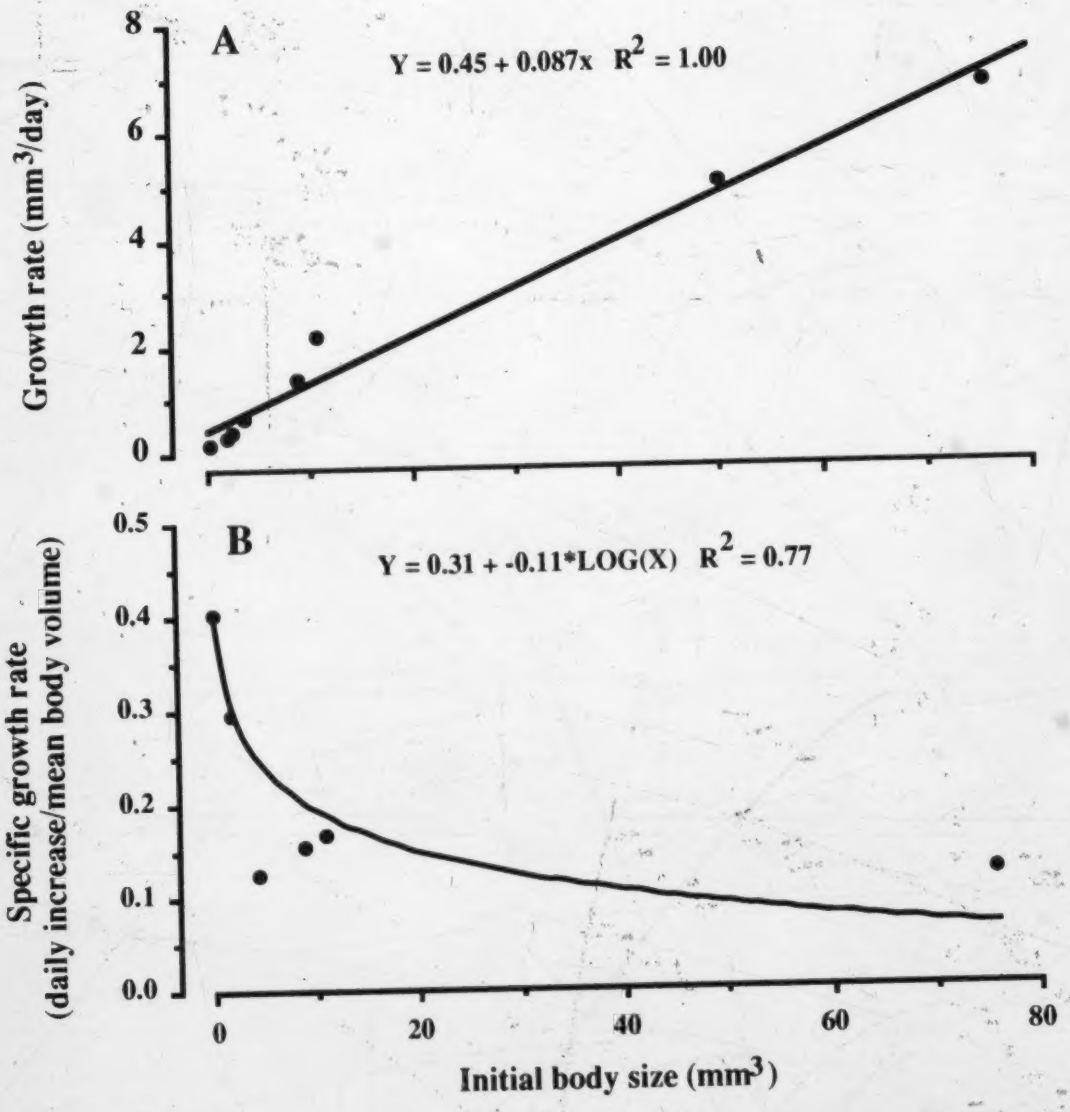


Figure II-10: Relationship between initial body size and growth rate of *Capitella* sp. measured *in situ*: A, daily increase in body volume; B, specific increase rate in body volume (daily net increase divided by averaged body volume at the beginning and the end of experiments).

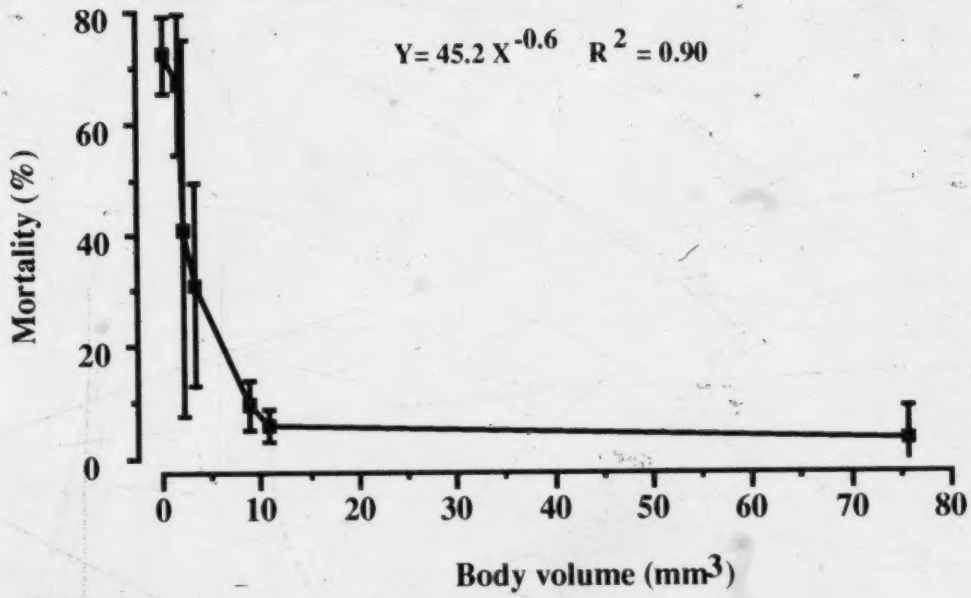


Figure II-11: Relationship between initial body size and mortality rate of *Capitella* sp. at the Grappler Inlet study site. The values plotted are mean ± standard deviation, for 12 replicate trays.

Table II-4: Recruiting rates of *Capitella* and other polychaetes in settling trays in Grappler and Bamfield Inlets. Values in the "# of recruits" column are mean ± standard deviation (sample size).

Experimental period	# of recruits	recruiting rate
	***Capitella* sp.**	
Grappler Inlet:		
Apr. 14 to May 4, 1988	720 ±796/m^2 (12)	34/m^2/day.
May 11 to Jun. 2,1988,	1182±661/m^2 (6)	56/m^2/day
Jun. 13 to Jul. 3, 1988,	169±40/m^2 (12)	8/m^2/day
Jul. 5 to Jul. 26,1988	399±36/m^2 (12)	19/m^2/day
Bamfield Inlet:		
May 10 to Jun. 7,1988	917±520/m^2 (6)	31/m^2/day
	Other polychaetes found in trays in Bamfield Inlet (May 10 to Jun. 7, 1988)	
Armandia brevis.	6329 ±1820/m^2 (6)	211/m^2/day
Polydora ligni	4142±1717/m^2 (6)	138/m^2/day
Polynoid spp.	1396±425/m^2 (6)	46.5/m^2/day

Other polychaetes such as *Armandia brevis*, *P. ligni*, and *polynoid* spp. occurred in the trays at higher densities than *Capitella*. There were 6329 ±1820 *Armandia brevis*/m^2 (6 replicate trays), 4142±1717 *Polydora ligni*/m^2 (6 replicate trays), and 1396±425 *Polynoid* spp./m^2 (6 replicate trays) found in that same period. The calculated recruiting rates for these three species were 211/m^2/day, 138/m^2/day, and 46.5/m^2/day respectively. *Armandia brevis* and *Polynoid* spp. are epifaunal species while *P. ligni* is an infaunal species. Most of the individuals found in the trays were newly-settled juveniles.

However, the intensive settlement of *Capitella* sp. in Bamfield Inlet did not establish a new adult population, which indicated high post-settling mortality. It appeared that predation contributed most to the mortality of post-settling stages in Bamfield Inlet. Juveniles in Bamfield Inlet and at the Grappler Inlet study site had similar mortality when they were maintained in trays without the presence of predators. It was found that the mortality rate of newly-settled juveniles was 3.1±1.3%/day (three replicate trays) in Grappler Inlet, which was similar to 3.0±0.1%/day for three settling trays in Bamfield Inlet (Mann-Whitney test: U=3.0, P=0.33); the mortality rate of two-week-old juveniles was also similar at 1.48±0.87%/day (three replicate trays) for Grappler Inlet and 1.25±0.37%/day (three replicate trays) for Bamfield Inlet (Mann-Whitney test: U=0.0, P=0.096).

Figure II-12A summarizes the size distribution of juveniles collected in the trays placed at the Grappler Inlet study site from May to August of 1988. New recruits collected on May 4, 1988 were very small. According to laboratory and field growth experiments, the body volume of newly-hatched and newly-settled juveniles of *Capitella* sp. averaged about 0.15-0.17 mm^3. Since these juveniles had a growth rate of 0.4 mm^3/day (Fig. II-8A) they should reach a size larger than 12 mm^3 in 3 weeks. Thus, it is

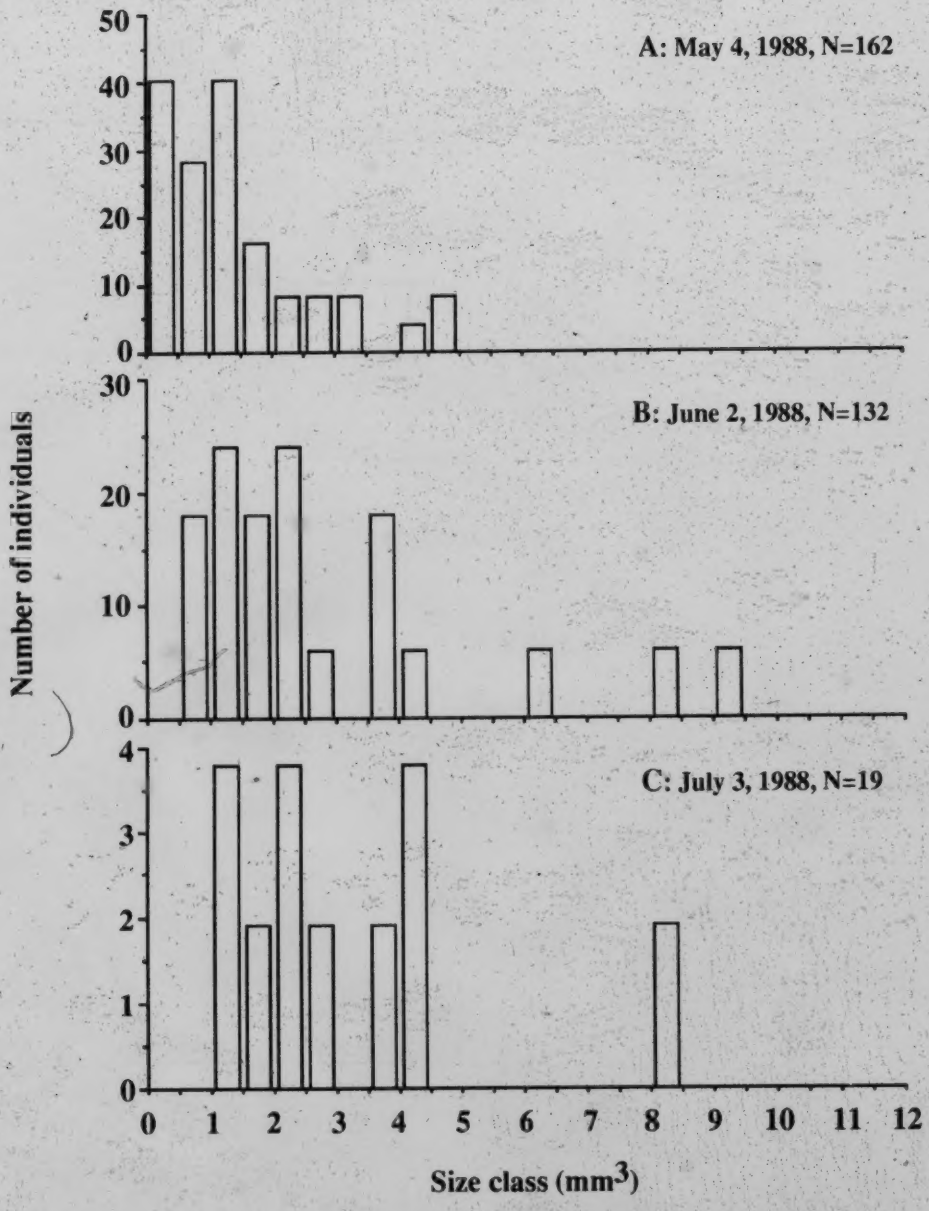


Figure II-12A: Size distribution of newly-recruited juveniles of *Capitella* sp. in the experimental trays at the Grappler Inlet study site. The trays were placed in the field from April 14 to May 4 (A), from May 11 to June 2 (B), and from June 12 to July 3, 1988 (C)

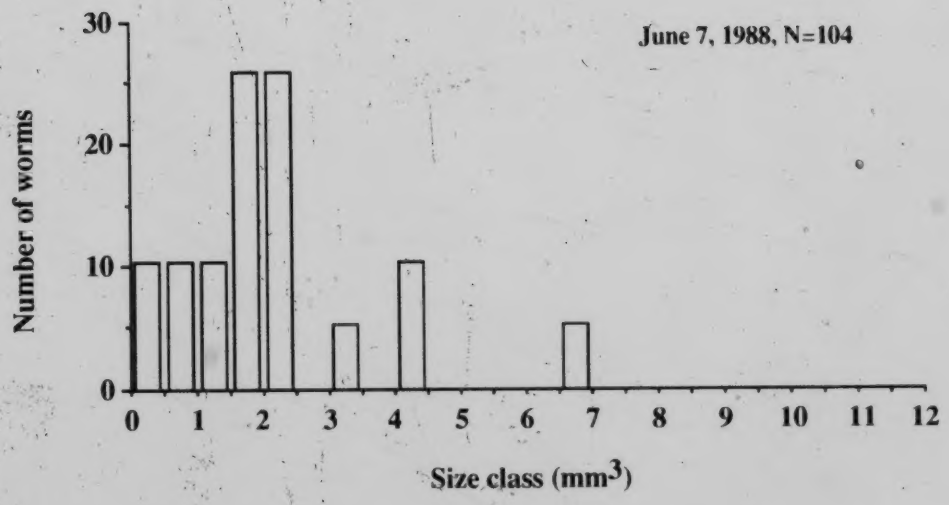


Figure II-12B: Size distribution of newly-settled juveniles of *Capitella* sp. in the experimental trays at the Bamfield Inlet study site. The trays were placed in the field from May 10 to June 7, 1988.

concluded that the approximately 40% of new recruits that had a body volume of less than 1 mm^3 must be newly-settled juveniles and were no more than 3 weeks old. In the samples from June and July, new recruits can be divided into at least two or three cohorts. The animals with a body volume larger than 6 mm^3 were the oldest that must have settled at the beginning of the experiment. Figure II-12B shows the size distribution of juveniles in the experimental trays from Bamfield Inlet during a period of 3 weeks (from May 10 to June 7). Over 50% of these new recruits had a body volume of less than 2 mm^3, indicating that they were newly-settled juveniles.

d. Fecundity

Animals of cohorts A and B in the experimental trays reached sexual maturity within 2.5 months. By July 3, 1988, among 162 individuals, 12 were males, three were hermaphrodites, and the rest were females. By July 27, 42 females released eggs with an average volume of $7.26 \pm 0.01 \times 10^{-3}$ mm^3 /egg (range: 5.53-10.1, N=220 eggs). The average dimensions of these eggs were 269.1 ± 32.1 µm (range: 220-314 µm) and 227.0 ± 24.4 µm (range: 195.8-265.6 µm) for the long and short axes respectively. In terms of the number of eggs produced in the first spawn of each individual, the average fecundity of the 42 females was 764 ± 207 (range: 322-1172). Eggs in some tubes developed to larvae that emerged from the tube and swam close to the bottom of the culture beaker for about 24 hours prior to settling. Newly-settled juveniles from these larvae did not differ in either size or morphological features from the juveniles crawling out of adult's tubes.

Another important finding was that 5 females produced very small eggs with an average volume of $0.63 \pm 0.40 \times 10^{-3}$ mm^3 (N=60). The average dimensions of these eggs was 104.3±23.3 µm for the long axis and 103.7±22.5 µm for the short axis. Average fecundity of these five animals was 6890±3116 eggs/first spawn/worm. The egg energy content of the small eggs was 8.58 ±1.56 microjoules/egg. As mentioned previously, juveniles used for these field experiments were all siblings. What triggered these 5 animals to switch their reproductive mode will be discussed in the next 4 chapters,

in which the effects of food and aging on the reproductive characteristics will be examined.

7. The effect of drifting seaweeds on mortality

Cage experiments revealed that the mortality of *Capitella* in different size classes was affected not only by their size (two-way ANOVA test: $F=41.4$, $P<0.001$) but also by the cages (two-way ANOVA test: $F=54.9$, $P<0.001$). Animals in trays without cage cover had about 20 to 30% higher mortality than animals in trays with cover protection (Figure II-13). This indicated that drifting seaweed is a factor in animal loss (mortality). However, the high mortality of juveniles and young adults in trays with cages indicated that factors other than drifting seaweed may play even a greater role in contributing mortality.

8. Laboratory predation experiments

a. Predation by pelagic predators

Prey density had a significant effect on the predation rates of three pelagic predators on the trochophores of *Capitella* (Fig. II-14A, two-way ANOVA: $F=58.35$, $P<0.001$). The predation rate increased with increasing prey density for all three predator species. Species-specific differences in the predation rates on trochophores of *Capitella* were evident in the slopes of functional response curves (Fig.II-14A, two-way ANOVA: $F=88.76$, $P<0.001$). Among the three species of predators, juvenile squid (*Loligo* sp.) had the highest predation rate, while the zoeae of *Hemigrapsus oregonensis* had the least impact. There was no interaction between species of predators and prey density (two-way ANOVA: $F=24.19$, $P<0.001$).

The clearance rate of the three predators was also species-specific. There was no linear relationship between initial prey density and clearance rate in juvenile squid. The clearance rate increased with increasing prey density, reached a maximum point at a density of 100 prey per liter, and then fluctuated (Fig. II-14B). For zoeae of *Petrolisthes*

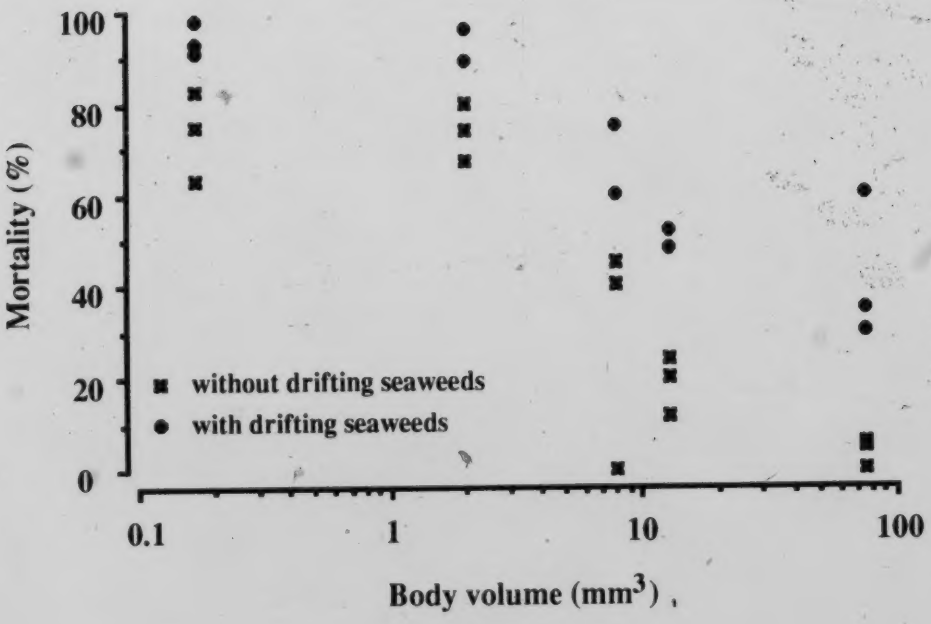


Figure II-13: The effects of drifting seaweeds and body sizes on the mortality of *Capitella* sp. at the Grappler Inlet study site. Seaweeds were excluded by using metal cages to cover the experimental trays.

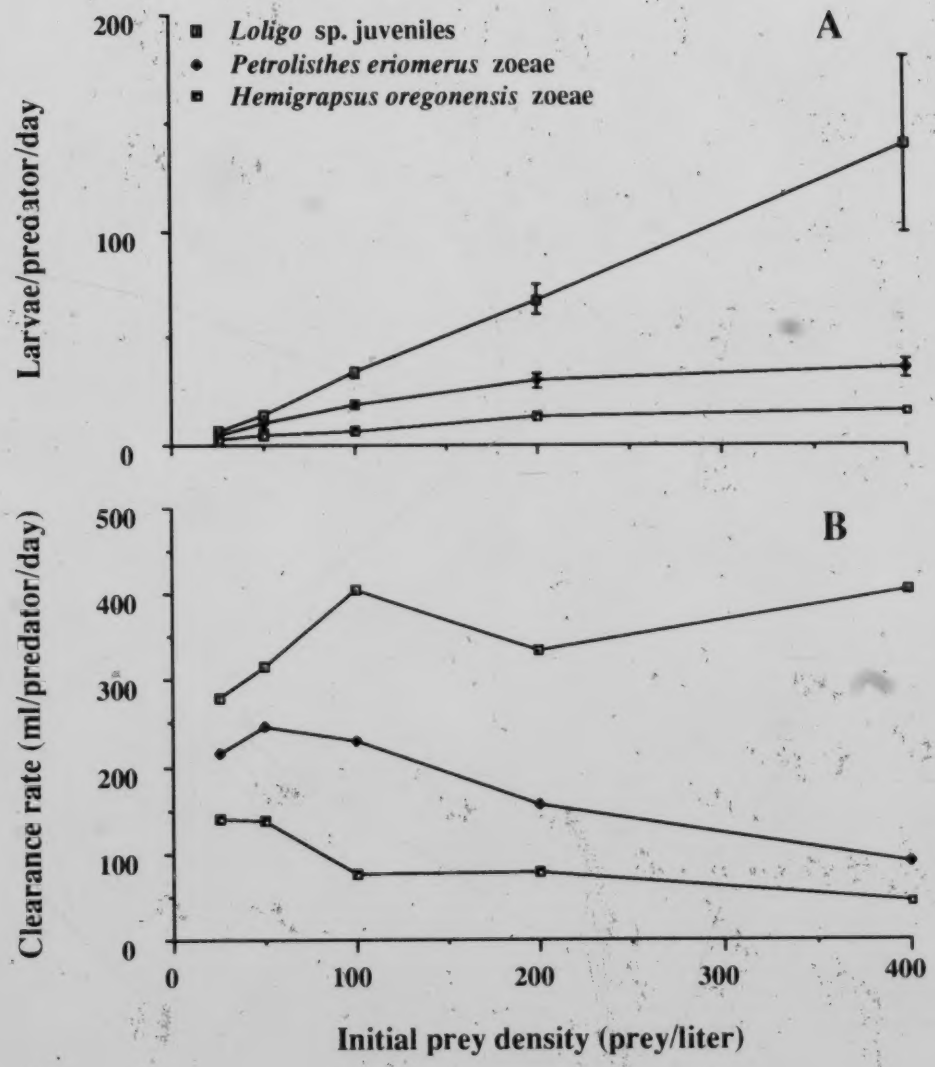


Figure II-14: Predation by pelagic predators on trochophores of *Capitella* sp. A, predation rate (the values plotted are mean ± standard deviation of four replicates; B, clearance rate (the values plotted are averaged clearance rate).

eriomerus, the clearance rate increased slightly at initial prey densities between 25 and 100 prey per liter, decreased with increasing prey density, and the functional response curves were reverse linear. For larval *H. oregonensis*, the clearance rate decreased with increasing initial prey density (Fig. II-14B).

b. Benthic predation

The adult benthic predator *Polydora ligni* had significantly greater ingestion rates on trochophores and settling-stage larvae of *Capitella* than had they on competent-stage larvae, and juveniles. Consequently, the slope of the response curve for trochophores and settling larvae was significantly greater than the slope for juveniles and competent larvae (Table II-5, Fig. II-15A, two-way ANOVA: $F=267.53$, $P<0.001$). *P. ligni* ingested competent larvae and juveniles at a higher rate than did pelagic predators, indicating that this benthic predator may greatly reduce the numbers of settling and post-settling of *Capitella* sp. (Fig. II-15A). Overall losses of larvae were much less in all control treatments, indicating significant predation effects on all developmental stages of *Capitella* sp. The rate of predation by *P. ligni* also increased with increasing prey density (Fig. II-15A, Table II-5, two-way ANOVA: $F=3740.3$, $P<0.001$).

Differences in the rate of clearance by *P. ligni* were significant during feeding experiments conducted with different developmental stages of *Capitella* (Table II-6, Fig. II-15B, two-way ANOVA: $F=3.70$, $P<0.05$). However, the clearance rate was unaffected by the initial prey density (two-way ANOVA: $F=1.76$, $P>0.05$); this was mainly due to the large variation among different stages and within each stage. For trochophores, clearance rates increased at initial prey densities between 25 and 50 per liter and then decreased rapidly (Fig. II-15B). For settling larvae, the clearance rate fluctuated around 50 ml/predator/day (Fig. II-15B). There were no trends in clearance rates of competent larvae and juveniles.

Stage-specific differences in predation rates (Fig. II-15A) reflected not only differences in the susceptibility (due to size, behavior, and swimming speed of prey) of

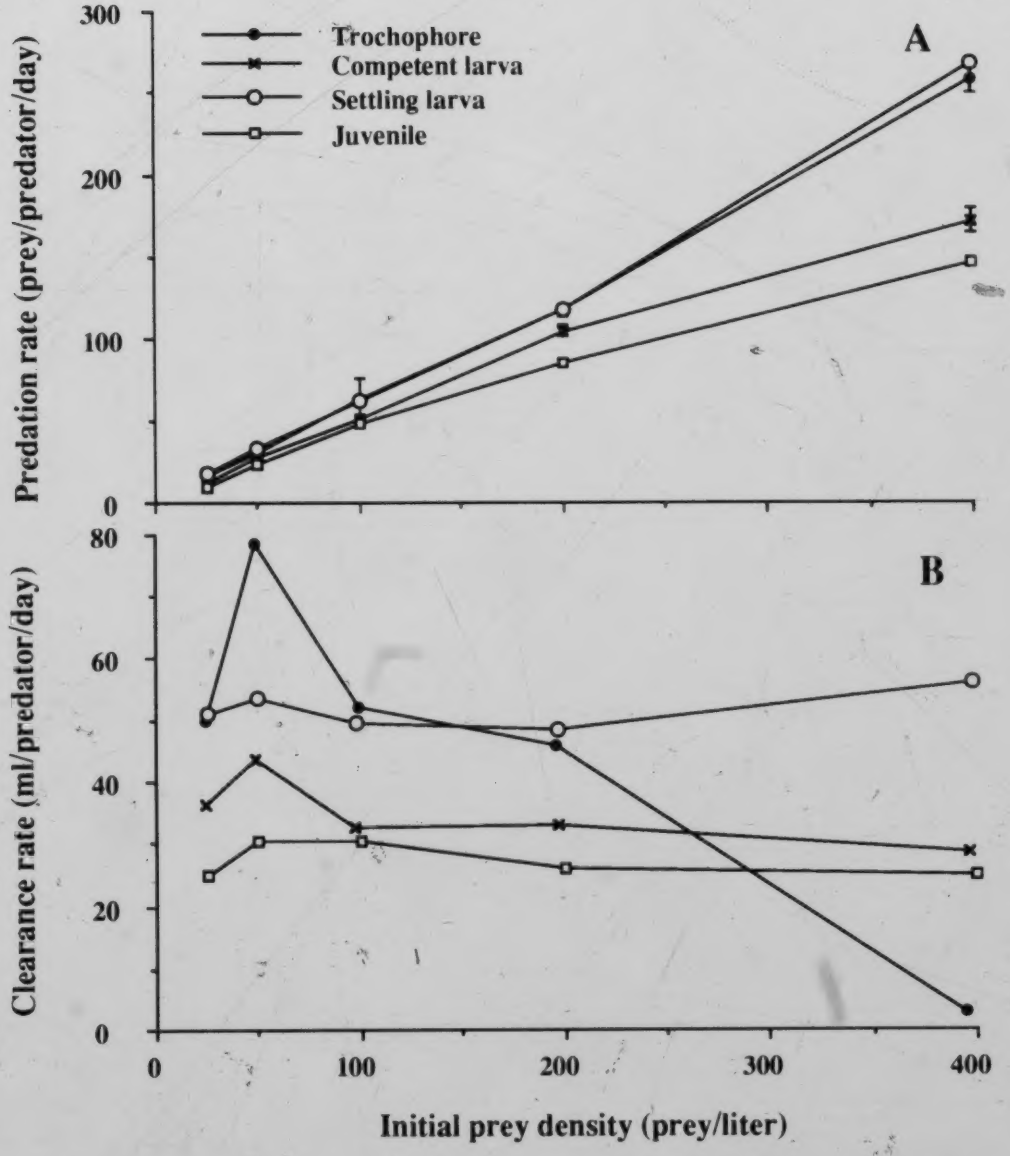


Figure II-15: Predation by benthic predator, *Polydora ligni*, on trochophores, competent larvae, settling larvae, and juveniles of *Capitella* sp. A, predation rate (the values plotted are mean ± standard deviation of four replicates); B, clearance rat (the values plotted are averaged clearance rate).

Table II-5: Results of single-factor ANOVA tests of the effects of prey density on predation rates of *Polydora ligni* on trochophores, competent larvae, settling larvae, and juveniles of *Capitella* during the feeding experiments.

Prey Stage	Source	SS	MS	DF	F-ratio	P
Trochophores	Density	149674.7	37418.7	4	489.24	P<0.001
	Error	1147.3	76.5	15		
Competent larvae	Density	68328.8	17082.2	4	896.7	P<0.001
	Error	285.8	19.1	15		
Settling larvae	Density	167829.2	41957.3	4	7492.4	P<0.001
	Error	84.0	5.6	15		
Juveniles	Density	44359.2	11089.8	4	1895.7	P<0.001
	Error	87.8	5.9	15		

Table II-6: Results of two-way ANOVA tests of the effects of prey density on predation rates of *Polydora ligni* on trochophores, competent larvae, settling larvae, and juveniles of *Capitella* during the feeding experiments.

Source	SS	MS	DF	F-ratio	P
Between density	400147.5	100036.9	4	3740.3	P<0.001
Between stage	21465.7	7155.3	3	267.5	P<0.001
Interaction	30044.5	2503.7	12	93.6	P<0.001
Error	1604.8	26.8	60		
Total	453262.4		79		

Table II-7: Results of two-way ANOVA tests of the effects of prey density on clearance rates of *Polydora ligni* on trochophores, competent larvae, settling larvae, and juveniles of *Capitella* during the feeding experiments.

Source	SS	MS	DF	F-ratio	P
Between density	1170.6	292.6	4	1.76	P>0.05
Between stage	1851.1	617.1	3	3.70	P<0.05
Error	2000.4	166.7	12		
Total	5022.1		19		

Capitella larvae and juveniles to predation, but also differences in the modes of feeding utilized by *P. ligni* to capture and handle prey (Table II-7).

P. ligni used one of its two feeding tentacles independently to search for, sort, and handle small food items, but used both tentacles to handle large food particles. Table II lists the handling time of *P. ligni* on different types of prey. Since the predation rate and handling time of *P. ligni* for each prey type were determined, it was possible to calculate the total time that a predator spends to ingest food. For example, at the initial prey density of 400 larvae per liter, the average rate of predation by *P. ligni* on the trochophores of *Capitella* was 259 larvae/day and the average handling time was 7.02 seconds per prey item. Hence, *P. ligni* only needs one-half hour to ingest 259 larvae. This indicates that the predator spends most of its time searching for food or digesting captured food. Laboratory observations in this study showed that the handling time of the predator was related to the size, morphological features, and behavior of the prey and the physical condition of the predator. For example, settling larvae of *Polydora* spp. lost their long swimming setae and usually crawled on the bottom of the culture beaker. These larvae were easy for the predator to capture, but the handling time for this kind of prey was long. Competent larvae of the same species possessed long swimming setae that are used in defense. After being caught by the predator, these larvae usually coiled into a ball so the long, protruding setae covering the whole body. This made it difficult for the predator to transfer these larvae to the mouth.

Table II-8: Relationship between prey size (body length) and handling time of *Polydora ligni*. The values are mean ± standard deviation (sample size).

Prey species	Prey size (μm)	Handling time (second)	Swimming speed mm/second
***Capitella* sp.**			
Trochophores	115.7±13.8 (30)	7.02 ± 2.49 (30)	
Settling larvae	445.6±38.2 (30)	12.87 ±5.43 (30)	crawling
***Polynoid* larvae**	258.3±24.2 (30)	5.23 ± 2.34 (30)	
***Polydora* sp.**			
9-setigers	591.5±38.6 (30)	8.95 ± 2.73 (30)	
15-setigers	784.7±48.2 (30)	8.31 ± 2.93 (30)	
Polydora polybranchia			
12-setigers	479±28.3 (30)	9.66 ± 3.09 (30)	18.4±4.9(20)
settling larvae	782±39.7 (30)	8.07 ± 2.75 (24)	crawling

D. DISCUSSION

The recruitment and population dynamics of *Capitella* sp. at the Grappler Inlet study site in Barkley Sound appeared to be controlled by a number of factors including the fecundity and reproductive activities of animals; the distribution and abundance of planktonic larvae; settling rates; the mortality of post-settling stages; the growth rate of post-settling stages; the intensity of predation on larvae by planktonic predators; the intensity of predation on competent larvae, metamorphosing larvae and juveniles by the benthic predators; the intensity of disturbance by drifting seaweed on the population, and especially on the newly-recruited juvenile. Some of these factors can be monitored by laboratory and field experiments. Although each of these factors was discussed here, the emphasis was placed on the impact of food availability and predation.

1. The relationship between environmental conditions and population density

The population density of *Capitella* sp. underwent seasonal changes in Grappler Inlet. The population density began to increase in the late spring and reached a peak in summer, then declined throughout fall. In winter and early spring, the density remained very low. These seasonal changes of population density appeared to be associted with the growth and availability of seaweeds such as *Ulva* and *Enteromorpha*. These green algae begin to grow when ambient seawater temperature increases to about 10°C in March; the biomass of these seaweeds increases gradually in the successive months and reaches the maximum in June or July to form thick mats on the surface of intertidal substrata. Bright sunshine and high temperature not only enhance the growth of these seaweeds but also accelerate their decay on the boundary layer between mud and seaweed mat. This provides food for *Capitella* sp. and other infaunal polychaetes.

Both laboratory and field observations have documented that an individual's growth, population size, and annual reproductive output of *Capitella capitata* are related to the quantity and the quality of food (Tenore 1975, 1977, 1981, 1983, Chesney and

Tenore 1985, Tenore and Chesney 1985, Brown *et al.* 1987, Tsutsumi 1987). In the field, *Capitella* are more dense in substrata with high organic content (Wu 1964, Bellan 1972, Reish 1974, Warren 1977, Kikuchi 1979, Yamamoto 1979, 1981, Tsutsumi 1983, 1987, Tsutsumi and Kikuchi 1983, 1984, Wu and Qian 1987a, 1987b, Wu *et al.* 1988). Laboratory experiments have indicated that this is related to the increase of fecundity, and/or the shortening of generation time, and/or the faster growth of *Capitella* spp. (Tenore and Chesney 1985, Grémare *et al.* 1988, 1989a). Very high resistance to low levels of oxygen and heavily polluted environments (represented by high concentrations of H_2S) has also been considered as the main reason for the success of *Capitella*. The population dynamics of *Capitella* were, in fact, characterized by early recolonization of azoic areas, and rapid population growth. At the Grappler Inlet study area, there was no evidence of pollution. The decay of seaweeds was the only apparent source that could contribute to a gradual build-up of organic material and low oxygen tension in the substratum. However, compared with the conditions at other study sites (Wu *et al.* 1988), this situation was very mild and lasted only a short time. This may explain why the population density in this area was much lower than those reported in previous studies (Wu 1964, Bellan *et al.* 1972, Reish 1974, Warren 1977, Kikuchi 1979, Yamamoto 1981, Tsutsumi 1983, 1987, Tsutsumi and Kikuchi 1983, 1984, Wu *et al.* 1988). Since the growth of the green seaweeds *Ulva* and *Enteromorpha* showed a distinct seasonality, the concentration of organic material should also parallel these seasonal changes. In fact, the pattern of population density change was associated with seaweed growth. From this point of view, it can be concluded that food limitation is one of the major controlling factors of the population dynamics of *Capitella*. Limited food sources in late fall and winter, combined with heavy predation by infaunal predators retarded the population growth of *Capitella*. Sexually mature individuals collected from the field were much smaller in body size than their offspring that were reared on ground seaweed in the

laboratory. This further indicates that populations in the field were limited by food availability and predators.

2. Reproductive activity

The population of *Capitella* sp. in Grappler Inlet reproduced throughout the year although the proportions of pre- and post-spawning individuals in the population changed seasonally. The peak of reproduction was correlated with seasonal changes in temperature and the nitrogen concentration in the water column. The seasonal growth of *Ulva* and *Enteromorpha* in this local community may control the amount of food available for *Capitella*, which, in turn, may control the reproductive activity of *Capitella*. However, there was no direct evidence to support this idea, since the organic concentration in the sediment was not studied. Nevertheless, it has been demonstrated in laboratory experiments that fecundity, generation time, egg size, and larval form are influenced by the quantity and quality of food.

3. Larval abundance and distribution

The density of polychaete larvae was significantly different among Grappler Inlet, Bamfield Inlet, Dixon Island, Dodger Channel, and Execution Rock. Polychaete larvae were consistently more abundant in Bamfield and Grappler Inlets than at the other three sampling sites. The general pattern of larval distribution in this area supported the hypothesis that larval density is higher inshore than offshore. These data also indicated that the main source of these larvae were adults located in Bamfield Inlet, Grappler Inlet, and in an area near Dixon Island, and that most of these larvae had limited capacity for dispersal. The distribution pattern of polychaete larvae in the study area was opposite to that of asteroid larvae, which are consistently more abundant in Trevor Channel than in shallow water near established populations of *Asterina miniata* in Grappler Inlet and Bamfield Inlet (Rumrill 1987). It has been suggested that metamorphically competent brachiolaria larvae most likely re-enter Bamfield and Grappler Inlets after a period of development in Barkley Sound; this movement is controlled by wind patterns and tidal

oscillations (Rumrill 1987). In contrast, winds and oceanic currents may have different effects on the dispersal of larval polychaetes. It is likely that northwest wind-driven surface currents and the formation of retrograde fronts may favor the retention of larvae on or near the adults' habitat in Grappler and Bamfield Inlets. Tidal circulation tends to create water mass oscillations that retain larvae in the adults' habitats (Cameron and Rumrill 1982, Levin 1981, 1983, 1984, 1986, Banse 1986). As a result, these physical factors limit dispersal of estuarine species and reduce advective loss of larvae. Equally important, abbreviated development and a short planktonic period, as well as demersal swimming favor larval retention in estuaries. Larvae of *Capitella* in this study had a short planktonic life, settled in 1 or 2 days, and almost all of the larvae collected from plankton samples swam close to the bottom of culture beakers. On the other hand, larvae of *Asterina* spent a much longer period in the plankton.

Polychaete larvae were also consistently more abundant in Bamfield Inlet than in Grappler Inlet. This may be because the larger mudflat area in Bamfield Inlet is inhabited by a very large polychaete community. Similarly, *Capitella* sp. larvae were more abundant in Bamfield Inlet than in Grappler Inlet and in the area near Dixon Island. However, the population density of *Capitella* in the intertidal area of Bamfield Inlet and Dixon Island was so low that a quantitative study could not be conducted. Such differences suggest that either variations in larval abundance and distribution may not contribute to the differential recruitment pattern of *Capitella* in the study area; or that some small population of *Capitella* existed somewhere subtidally or in deep water in this area.

The peak of larval abundance in the plankton in Grappler Inlet was coincident with the peak of phytoplankton blooming, and with the peak of reproductive activity. The relationship between larval abundance and reproductive activity was obvious

4. Larval settlement and recruitment

Differential larval settlement plays an important role in determining the recruitment and population dynamics of benthic marine invertebrates. Environmental cues and larval behavior at the settling stage can influence larval settlement and metamorphosis and determine eventual destinations, although larval transportation and deposition are largely controlled by hydrographic factors (Woodin 1986, Chia 1989). The density of *Capitella* spp. collected in collectors suspended in the water column was up to 1,000 times higher than that in collectors placed on the bottom, suggesting that larvae may act like passive particles in turbulent near-bottom flows (Hannan 1981, 1984). Previous studies have also indicated that settlement of *C. capitata* (*Capitella* spp.) larvae may be selective. Hydrogen sulphide used to be considered as a settlement cue for *Capitella* sp. I larvae (Cuomo 1985), but a recent study showed that is toxic to *Capitella* sp. I larvae, and that the stimulus implicated in the settlement of this species is a chemical cue associated with organic matter (Dubilier 1988). The results from this study show that *Capitella* sp. larvae collected at my study sites did not have a preference for mud collected from different localities in the field, indicating that their settlement is not selective. Field experiments also demonstrated that recruitment in Grappler Inlet was not significantly higher than in Bamfield Inlet, indicating that the differences in distribution and abundance of *Capitella* at these two sites is not due to differential larval settlement. It may be due to differential mortality of post-settling stages caused by predation and other factors.

Although the intensity of recruitment could be correlated with larval abundance in the plankton, recruitment of *Capitella* appeared to be controlled by other factors. Newly-settled juveniles were present in samples every month, but the numbers varied from sampling period to sampling period, with a peak of settlement occurring in the summer.

5. Predation upon larvae and juveniles

Predation on adults in soft-bottom marine habitats has been intensively studied (Ambrose 1984a, 1986, Zajac 1986). Relatively little is known about the importance of predation by benthic predators on larvae and juveniles, although a few studies have indicated potentially important influences on the recruitment of marine benthic invertebrates (Steinberg and Kennedy 1977, Highsmith 1982, Cowden *et al.* 1984, Rumrill *et al.* 1985, Rumrill 1987).

Laboratory and field experiments indicated that predation upon competent larvae, settling larvae, and juveniles of *Capitella* sp. does play an important role in influencing patterns of recruitment. First, *Capitella* larvae have no effective defensive structures against benthic suspension-, filtering-, and deposit-feeders, and there is little chance for these larvae to escape after being caught by benthic predators. Second, according to laboratory observations, *Capitella* larvae stay close to the bottom prior to settlement. This behavior would increase the encounter rate with benthic predators, and as has been shown in previous studies, competent larvae of many marine invertebrate species test the substratum before settling (Pawlik and Faulkner 1986, Rumrill 1987) Consequently, this increases the risk of being caught by benthic predators. Third, predation experiments in the laboratory have demonstrated that *P. ligni* feed on trochophores, competent larvae, settling larvae, and newly-settled juveniles of *Capitella* sp. Predation by *P. ligni* had highly significant effects on survival rate of *Capitella* larvae and juveniles in stage-specific and density-dependent predation experiments. The mortality of competent larvae and juveniles was low when compared with that of trochophores and metamorphosing larvae stages. *Polydora ligni* had higher ingestion rates on *Capitella* sp. larvae of different stages than any other pelagic predator tested in the laboratory. These results further suggested that benthic predators can be a major threat to larvae and juveniles of *Capitella*. Finally, my results demonstrated that there was intensive settlement in the experimental trays placed in the mudflat in Bamfield Inlet. However, there were few juveniles or adults

of *Capitella* found in the same region. The polychaete community in this particular site was dominated by suspension and deposit-feeding spionids. Such observations suggest that post-settling stages of *Capitella* sp. were eliminated by benthic predators and could not establish a population. Rumrill (1987) also found that asteroid larvae in Bamfield Inlet are exposed to a greater risk than those in Grappler Inlet due to differences in the type and number of suspension feeders. In conclusion, owing to the differences in benthic predator abundance, better recruitment of some marine invertebrates may occur in Grappler Inlet than in Bamfield Inlet.

The intensity of predation by benthic *P. ligni* on larvae or juveniles depended upon the potential interactions between foraging strategies of the predator and the prey defensive tactics. *P. ligni* is a common constituent of many intertidal and shallow subtidal infaunal and epifaunal communities (Zajac 1986). Like most spionids, this species builds a tube and feeds at the sediment-water interface by collecting surficial and suspended particles with grooved, ciliated tentacles. Any larvae or juveniles of *Capitella* that fall into the region covered by the two tentacles of *P. ligni* would be in danger of being ingested.

According to the optimal foraging strategies postulated by Greene (1986) and Greene *et al.* (1986), *P. ligni* is a typical ambush predator; its ingestion rate would be dependent upon the vulnerability of different prey types, which is, in turn, the product of the encounter rate and subsequent susceptibility (see below). It has been suggested that encounter rate can be positively correlated with the developmental stage, motility, size, and age of the prey (Greene 1986). In *Capitella*, young trochophores may have a low encounter rate with *P. ligni* since young trochophores stay away from the interface between the bottom and the water column. Although competent larvae have a larger body size and a better ability to swim, they may contact the predator more frequently during the period in which they test the substratum. Metamorphosing larvae and juveniles have the highest encounter rates and are more susceptible to predation.

Prey susceptibility is determined by the defensive behavior and size of the prey. *P. ligni* usually had difficulty in handling large juveniles. Rumrill (1987) categorized prey susceptibility to benthic predators and pelagic predators according to the following attributes: benthic predators are non-motile and large; not all developmental stages are exposed to the same risk, since predation by benthic suspension feeders is restricted largely to the periods of planktonic development shortly after spawning and during settlement; and the processes of larval settlement and predation by benthic suspension feeders both take place during the transition from three to two dimensional space within shear gradients associated with bottom boundary layers. This study shows that benthic predators can also prey on young juveniles and can directly affect recruitment rates in situations where a pelagic predator has little impact. In general, the influence of a benthic predator on the recruitment pattern of *Capitella* or sessile organisms would be greater than would the influence of a pelagic predator.

Handling time, an important factor affecting the ingestion rate and handling time of *P. ligni*, was species-specific. The handling time of *P. ligni* on *Capitella* sp. increased with prey size; but for some other prey species, the relationship between their size and handling time was reversed. This is mainly due to differences in the morphological features and defensive behavior of the prey. In general, predation on the competent larvae and juveniles by benthic predators may has an extensive effect on the population dynamics and recruitment of *Capitella* in the field.

6. Predation and population dynamics

Predation and naturally occurring disturbances can influence the recruitment patterns and the population dynamics of a variety of polychaetes (Woodin 1976, 1982, 1984, 1985, Oliver *et al.* 1982, Ambrose 1984,1986, Chesney and Tenore 1985, Zajac 1986, Beukema 1987). For instance, the abundance of predatory polychaetes such as *Nephtys hombergii* and *Glycera* spp. and the density of prey species including the polychaetes *Scoloplos armiger* and *Heteromastus filiformis*, is negatively correlated

(Beukema 1987). It has also been found that predatory polychaetes such as *Nereis virens* and *Glycera dibranchiata* play a significant role in structuring marine sediment ecosystems (Ambrose 1984). In laboratory experiments, *C. capitata* populations have been unstable even under stable conditions; however, reducing the number and size of breeding adults would stabilize the population density of *C. capitata* (Chesney and Tenore 1985). It has been postulated that physical disturbances can also affect population dynamics of *C. capitata* in the following ways: crushing of individuals (either adults, juveniles, or larvae); disturbance of individual activities essential to population growth (e. g., settlement of larvae, females brooding young); burial of food or small individuals such as newly settled juveniles; and washout of organic matter from trays (Chesney and Tenore 1985). Similarly, differential predation rates, along with physical disturbance, may be the main factors controlling declines in the population of *Capitella* at the Grappler Inlet study site in fall and winter. Body size of newly settled juveniles and even adults of *Capitella* sp., is within the range consumed by predators such as *Nereis* and *Glycinde*. The impact of drifting seaweeds on juvenile loss indicated that biological disturbance can influence juvenile survival or redispersal. In conclusion, predation by benthic predators, and physical and biological disturbances contributed to shaping the population in the field.

7. Differential mortality of post-settling stages

Differential mortality of post-settling stages is a very important factor in determining the abundance and distribution of benthic marine polychaetes. However, this relationship has not been examined closely because of the difficulty involved in sampling juveniles and aging animals in the field. In this study, a new method for marking and recapturing polychaetes was utilized, making it possible to study the differential mortality of juveniles and adults of *Capitella* sp. The results of field experiments demonstrated that mortality was size dependent for juveniles and adults of *Capitella* sp. Over 90% of newly settled juveniles were lost in the period of up to 14-21 days after assuming a benthic life style. The mortality of young juveniles with a body volume of less than 3 mm^3 was

highest, which was about 65%, and animals with a body volume greater than 10 mm^3 had a mortality rate of less than 5% during the same period of time. This suggested that the juvenile stage was the critical period. An increase in the survival of the immediate post-settlement stage would contribute to wider distribution and greater abundance of *Capitella* sp. It should be pointed out, however, that the mortality of post-settling stages reported here may not represent the real mortality in the field population since my experiments were conducted under controlled conditions where no competition or predation took place.

8. The impact of drifting seaweeds on recruitment and juvenile re-dispersal

Under laboratory conditions, the mortality of newly-settled juveniles was low (less than 10% in 2 weeks). This indicates that the heavy losses of juveniles in the field experiments were not entirely due to intrinsic causes but were the consequence of other factors. Physical disturbances by oceanographic processes can crush or wash away juveniles from the experimental trays. Drifting seaweed can enhance the redispersal of juveniles and even adults, but in the meantime drifting seaweeds can also increase the loss of juveniles and adults. The differences in mortality between trays covered with cages and trays without cage coverage became more obvious when the size of the experimental animals increased. Ólfasson (1988) suggested that drifting algal mats act as a larval filter and inhibit larval settlement on soft-bottom benthic communities, since during the peak period of settlement (June and July) settling densities of the bivalves *Macoma balthica, Cardium glaucum, Mya arenaria,* and *Nereis diversicolor* were very high in sediment without algal cover, while no recruits of these species were found beneath algae. He then postulated the following five possibilities to explain his results: (1) larvae may preferentially select clear areas, (2) the cage structure causes small-scale changes in the water-flow near the bottom, thus transported larvae are passively sampled, (3) differential mortality could occur due to anoxic conditions beneath the algae, (4) differential mortality could also occur due to the absence of predators inside cages, and (5) algae act as a filter

for settling invertebrate larvae; he rejected the first four possibilities. My results suggest that seaweed mat may not only inhibit larval settlement but also cause juvenile and adult redispersal. To conclude, drifting seaweed in the intertidal zone indeed interferes with the juvenile recruitment of soft-bottom marine animals.

9. Growth of post-settling stages in the field

One common problem in studying polychaete ecology in the field is to age the animals collected from the field because of a lack of information about growth rate. Tenore (1975, 1979, 1981, 1985) has demonstrated in laboratory experiments that the growth of individual *Capitella* was not only controlled by the quantity and quality of food, but also by population density and possibly other factors. The growth of individual *C. capitata*, however, has never been measured *in situ* before. In this study, marking and recapturing infaunal polychaetes and measuring the growth of the *Capitella* sp. at the Grappler Inlet study site were conducted for the first time. In the first three months *Capitella* showed a rapid individual growth in the field. In general, the growth rate was positively correlated with the initial body size of the experimental animals. The highest growth rate, which was displayed as a sudden elevation along the growth curves, occurred just before the animal reached sexual maturity.

The effect of gametogenesis on increase in body size could not be detected on growth curves (see Chapter V). Also, the size difference among groups with different initial body sizes was amplified when animals grew. This indicates that slight differences in the spawning time or settling time may result in cohorts of different sizes. Therefore, it is very important to age animals and classify the cohorts collected from a field population. The growth rate recorded from the field in this study were much lower than those from Tenore's experiments, in which maximum daily individual growth rates of 21, 19, and 15% were recorded for small, medium, and large *Capitella capitata*. However, the growth rate of animals in the field was quite similar to that of siblings cultured in the laboratory on 2 mg dry ground *Ulva* spp./day/worm.

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CHAPTER III

COMPARISON OF LIFE HISTORY STRATEGIES WITH EMPHASIS ON THE EFFECTS OF AGING ON REPRODUCTIVE CHARACTERISTICS

A. INTRODUCTION

Capitella capitata, collected from the United States, has been divided into a complex of ten sibling species by some recent research (Grassle and Grassle 1976, Grassle 1980, 1984). The classification of the sibling species was largely based on differences in isoenzyme electrophoresis and variable reproductive characteristics such as: egg size and egg shape, fecundity, sperm morphology, duration of life cycles, breeding season, larval morphology, and larval development modes. The reproductive variation of *C. capitata* within a population and among populations, however, has not been carefully examined.

The first part of this chapter was designed to compare fecundity, egg size, egg energy content, reproductive effort, and larval developmental modes of the field populations since this thesis focused on the variability of reproductive characteristics of *Capitella* in Barkley Sound.

Several small populations of *Capitella* have been found in Barkley Sound, British Columbia. One group of *Capitella* resided in the squid egg capsules that scattered subtidally at the adjacent areas of Bamfield Marine Station. Animals in this group had large body size, produced many eggs that were very small and contained very low energy content. Eggs developed in adults' tubes for one week into small trochophore larvae that were planktotrophic and spent more than three weeks in the plankton. Animals of the

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second group were scattered at extremely low density in the mudflats in Bamfield and Grappler Inlets and did not form large populations. Therefore, it was difficult to conduct studies on the population dynamics of this group. Animals in this group had smaller body size and lower fecundity (5-7 times lower) than those from squid egg capsules. Animals produced larger eggs than did those from squid egg capsules; their eggs also developed into planktotrophic larvae that spent about 2 weeks in the plankton. The third group was found in mudflats in Grappler Inlet, and population dynamics of this group has been reported in Chapter II. Animals in this group had more setigers than those of other two groups, and produced the fewest eggs. However, their eggs were the largest and had the highest energy content. Eggs developed into lecithotrophic larvae, which developed into juveniles in adults' tubes or emerged at the 15 to 18 setiger stage from the tubes and swam for a short time before settling. Although juveniles from these three groups can not be separated, the adults can be separated arbitrarily based on differences in habitats and some morphological characteristics. Animals with lecithotrophic development were separated from those with planktotrophic development based on the differences in ovum size, number of ova per ovary, and egg size. Planktotrophic developers from subtidal squid egg capsules and intertidal mudflats were separated, based on the differences in habitats, body size, fecundity, egg size, larval size, and larval life-span.

The second part of this chapter assesses the effects of aging on fecundity (defined as the number of eggs per spawn), egg size, egg energy content, total reproductive output (defined as the total energy invested in eggs per spawn, and as the total volume of eggs produced per spawn) of *Capitella* sp. with lecithotrophic and planktotrophic development under controlled laboratory conditions.

Studies on the effects of aging on an animal's fecundity, egg size, and egg energy content are restricted mostly to studies of vertebrates (Green 1966, Pianka and Parker 1975, Calow and Woollhead 1977, Crawford 1980, Furness 1983, Duncan 1986). It has

been reported that the fecundity (litter size) of mammals changes with reproductive season and age (see review by Sadleir 1969). In fish, Kuznetsov (1973) found that the fecundity of the fish *Abramis brama* (L.) increased with age but the lipid content in the egg was reduced; egg diameter and weight fluctuated insignificantly. Lee (1981) reported that egg diameter of *Sillago sihama* varied with the age. Kaev and Kaeva (1986) found that egg size and fecundity increased with age in pink salmon, while egg size increased but fecundity decreased with age in chum salmon. Henrich (1988) found that the number of offspring in the first brood of the fish, *Heterandria formosa*, is negatively correlated with the remaining life span. It is noted that all of these data are based on observations of field populations. In marine invertebrates, the effects of aging on reproductive characteristics have not been determined although there is information, which may be associated with aging, scattered in the literature (Åkesson 1982, Peterson 1986, Bricelj *et al.* 1987, Levin *et al.* 1987, Wu *et al.* 1988). Generally speaking, no one has been able to determine the effects of aging on egg size, egg energy content, and total reproductive output per spawn, or to document the changes in these reproductive parameters over the life-time of individual animal. Thus, variations in the reproductive parameters during aging among siblings have never been demonstrated.

Previous life-table studies of marine invertebrates utilized number of eggs (offspring) to calculate reproductive values (Åkesson 1982, Levin *et al.* 1987). These, however, do not consider the changes of offspring quality with age, and simply assume that egg quality is constant through the entire life span. Based on the information on vertebrates, I would predict that reproductive values given in previously published life-tables may have overestimated the reproductive capacity of those species.

B. MATERIALS AND METHODS

1. Reproductive characteristics

In order to quantify the differences in reproductive characteristics of *Capitella* in Bamfield, Barkley Sound, British Columbia, pre-spawning individuals were collected. Animals in squid egg capsules were collected by SCUBA from Bamfield Inlet near the Government's Dock at 8-15 m depth and by dredging from Trevor Channel, Barkley Sound at about 60 m depth. Animals from intertidal populations with lecithotrophic and planktotrophic development were collected from intertidal mudflats in Grappler Inlet and Bamfield Inlet by sieving sediment through a 200 μm mesh. All animals from intertidal mudflats were maintained in separate culture beakers in the laboratory at Bamfield Marine Station at 10±1°C, and fed with ground *Ulva* spp. Animals in squid egg capsules were kept in a 25 l aquarium, so that they could continue to feed on squid egg capsules before spawning. Individuals that spawned in the laboratory within 4 days were used to assess their reproductive characteristics.

In the laboratory, once an animal began to release eggs in its tube, the worm was transferred to a clean beaker. The worm was removed from its tube just after all the eggs had been released from its coelom. The adult tube, with newly-released eggs, was then carefully opened, and the number of eggs was counted under a dissecting microscope.

The long and short axes of twenty to thirty newly-released eggs from each spent individual were measured with a Zeiss compound microscope equipped with an ocular micrometer. Egg volume (V) was approximated using the following formula: $V=(4/3)\pi A^2 B$, where **A** and **B** are the length of short and long axes of the egg respectively. Total volume of the released eggs per spawn was obtained by multiplying the number of eggs by mean egg size of that spawn.

Energetic content of the eggs was measured using the procedure described by Parsons *et al.* (1984) and McEdward (1986). Three replicates from the same female were used, each containing either 150 or 500 eggs, depending on egg size. Eggs were briefly

rinsed in distilled water to remove salts, incubated in concentrated (70%) phosphoric acid (1 ml, 15 min, 100-110°C) to remove residual chloride, then oxidized with potassium dichromate (0.484%) in concentrated sulfuric acid (2 ml, 15 min., 100-11°C). Reduction of the dichromate concentration indicated the amount of organic carbon oxidized. Samples were diluted (3.5 ml distilled water) and measured spectrophotometrically (at 440 nm). The organic content was reported as the weight of glucose (μg) yielding equivalent reduction in dichromate concentration. The resolution of the assay was approximately 5 μg^C. Organic carbon can be converted to joules by the formula: **1 μg^C=3.9x10^{-2}** Joules based on constants in Parson *et al.* (1984). The total energy of the released eggs was obtained by multiplying the number of eggs by the energetic content per egg.

To determine larval pelagic period of planktotrophic larvae, newly-hatched trochophores were reared in the laboratory at 10± 1°C (close to ambient seawater temperature in the study area) and fed a mixture of ground *Ulva* spp. (<50 μm particle size) and phytoplankton collected from the Bamfield Inlet. The duration from trochophore to settling stage was recorded. Body length of the newly-metamorphosed juveniles was measured, after they were relaxed in 0.36 M $MgCl_2$ solution.

2. Reproductive effort

Each of fifty-one females with lecithetrophic development cultured in the laboratory were dissected under a dissecting microscope as soon as an individual finished the first spawning. Gonadal tissues were separated from body tissue. Energy content in the body tissue and gonadal tissue as well as in the newly-released eggs in the tube were then assessed following the method described by McEdward (1986) and Peason *et al.*(1982). The proportion of energy in each part was calculated as the percentage of total energy of a whole animal.

The energy content in gonadal tissue, body tissue and the released eggs of 17 females collected from squid egg capsules were also assessed.

Because of the difficulty of separating small ovaries from somatic tissue, only total energy content in both newly-released eggs and body of 22 planktotrophic developers from intertidal habitats was assessed in the way described above.

Reproductive effort was calculated as the proportion of energy invested in newly-released eggs against the total energy content. Residual reproductive value was indicated by the proportion of energy in developing gonads remaining in the animal's body after spawning.

3. Effect of aging on some reproductive characteristics

Laboratory culture conditions were maintained as constant as possible in terms of food quality, sediment, and seawater throughout the experiments. Sediments used in this experiment were collected from an intertidal mudflat in Grappler Inlet, sieved through 200 μm mesh, washed in tap water for over 24 hours, dried outdoors in summer sunlight, and stored in plastic bags for later use in the experiments. Food was prepared from *Ulva lactuca*, which was collected from intertidal regions of Grappler Inlet in June 1987. The seaweed was washed with filtered seawater (50 μm) in the laboratory, rinsed quickly with distilled water, freeze-dried, and then grounded with an electric mill into fine powder (particle size is smaller than 50 μm). Finally, the powder was stored in a plastic bag. Seawater used in the experiment was filtered at 0.45 μm with a millipore filter.

Experiments were conducted on fifty sibling juveniles obtained from a single spawn of a single *Capitella* sp. with lecithotrophic development. Isolated juveniles developed into adults that can produce viable offspring without the participation of other individuals. Laboratory experiments have indicated that those individuals are hermaphrodites without male copulating spines (Qian and Chia 1991). Therefore, the experiments were simplified because all reproductive investment in a single spawn was from a single individual.

For planktotrophic developers, 20 pairs (one male and one female) of young adults (about 2 month old) from a single spawn of a females with planktotrophic

development of *Capitella* sp. were used. I did not consider the reproductive output of the male (through sperm transferring and copulation) during the analysis of final results because it is impossible to measure it.

Each juvenile of a lecithotrophic developer or each pair of young adults of a planktotrophic developer was placed into a 250 ml culture beaker which contained a 3 cm thick layer of sediment. The culture beakers were maintained in a shallow (10 cm deep) seawater table at 10-11°C in the laboratory. Animals were provided with a prepared diet of 2 mg dry weight/worm/day. The water in each beaker was partially changed (half of total volume) every day.

Fecundity, egg size, egg energy content , total egg volume and total energy content/spawn were recorded for each spawn of spent individuals. The methods for determining these reproductive parameters were the same as that in part **1**. Number of spawns, total fecundity, and total reproductive output in life-time were averaged from all the individuals with the same type of development.

4. Data analyses

One-way ANOVA and Student-Newman-Keuls (SNK) tests were used to compare the differences in reproductive characteristics among groups with different development models. One way ANOVA and unpaired t-test were used to assess the influence of reproductive patterns on reproductive effort. Non-parametric Kruskal-Wallis test and Non-parametric multiple comparison test (Mann-Whitney U test) were used to assess the effect of age on fecundity, egg size, egg energy content, and total reproductive output of planktotrophic developers (Zar, 1984).

The non-parametric Kruskal-Wallis test and Joint-Rank Ryan (JRR) test were used to assess the effect of age on fecundity, egg size, egg energy content, total egg volume/spawn, and total energy (joules) /spawn of lecithotrophic developers. Since large variations of each characteristic among individuals affected the results of the above tests, a correction was made for each individual, in which each parameter in the first

spawn was considered as 100%, the proportional changes in the successive spawns of an individual were calculated against the first spawn. Thus, anything smaller than 100% would show a decrease. The non-parametric Kruskal-Wallis test and JRR test were also used to test the effect of age on the percentage changes in each reproductive parameter among spawns.

For each parameter, the value of previous spawn (X value) was plotted against that of the following spawn (Y value) of each individual. Thus, any value above the diagonal line (zero increase line) indicates an increase, on the line indicates no change, and below the diagonal line indicates a decrease between two spawns. The number of animals that showed a decrease in each parameter was compared with the number of animals that showed an increase in the successive spawns with the G-test.

C. RESULTS

1. Reproductive characters of *Capitella* in Bamfield area

Reproductive characteristics of *Capitella* with three different developmental modes in the Bamfield area were summarized in Table III-1. Fecundity, egg size, egg energy content, and total egg energy invested in the released eggs per spawn were significantly different among three modes (Table III-1; SNK test, $P<0.05$). Animals from squid egg capsules produced about 7 times more eggs than planktotrophic developers from intertidal mudflat and 55 times more than lecithotrophic developers from intertidal mudflat. The egg size of lecithotrophic developers, however, is about 30 times larger than that of planktotrophic developers from squid egg capsules and and 13 times larger than that of planktotrophic developers from intertidal mudflat (Table III-1). Figure III-1 demonstrates diagrammatically the life-history cycle of *Capitella* sp. found in Bamfield area.

The egg energy content was positively related to egg size when data from three developmental modes were pooled (Fig. III-2A, $P<0.001$); whereas there was no relationship between egg size and egg energy content within a developmental mode

Table III-1: Reproductive characteristics of *Capitella* sp. from Bamfield area with the results of one-way ANOVA and Student-Newman-Keuls tests. Values that differ at the 0.05 level are joined by a solid line. Values are mean ± standard deviation (sample size). Here, lecithotrophic developers were collected from intertidal mudflat in Grappler Inlet, planktotrophic developers were collected from mudflat in Grappler and Bamfield Inlets and from subtidal squid egg capsules.

Development type	Lecithotrophic	Planktotrophic	Planktotrophic	ANOVA		SNK-test
	A (intertidal)	**B** (intertidal)	**C** (subtidal)	F	P	Difference
Egg diameter (µm)	285±17 (560)	123±16 (840)	94±16 (500)	87.5	<0.001	A B C
Egg volume (mm^3*10^{-3})	12.7±2.6 (560)	0.97±0.27 (840)	0.44±0.08 (500)	690.4	<0.001	A B C
Fecundity (eggs)	627±88 (28)	4991±4173 (42)	34353±22325 (25)	90.8	<0.001	A B C
Microjoules/egg	64.35±6.63 (28)	18.7±3.9 (42)	5.07±0.78 (25)	1535	<0.001	A B C
Joules/spawned eggs	40.11±5.05 (28)	91.24±78.23 (42)	167.47±108.83 (25)	8.2	=0.001	A B C
pelagic period	No-1 day	1-3 weeks	>>3 weeks			
Juvenile length (µm)	660-750	310-490	275-350			
Larval life-span	3 weeks	1 month	>1 month			

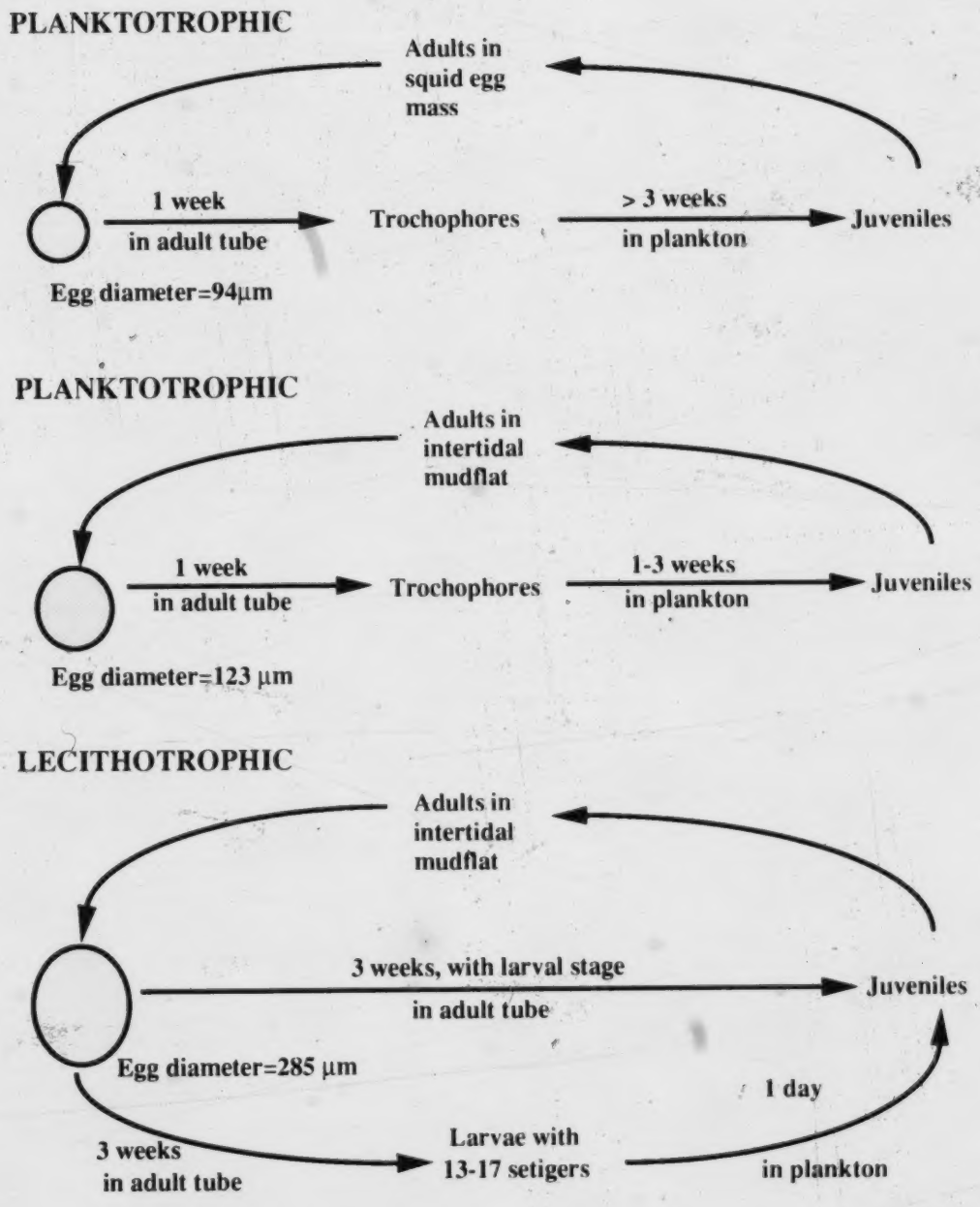

Figure III-1: Patterns of development found in *Capitella* sp. in Bamfield area.

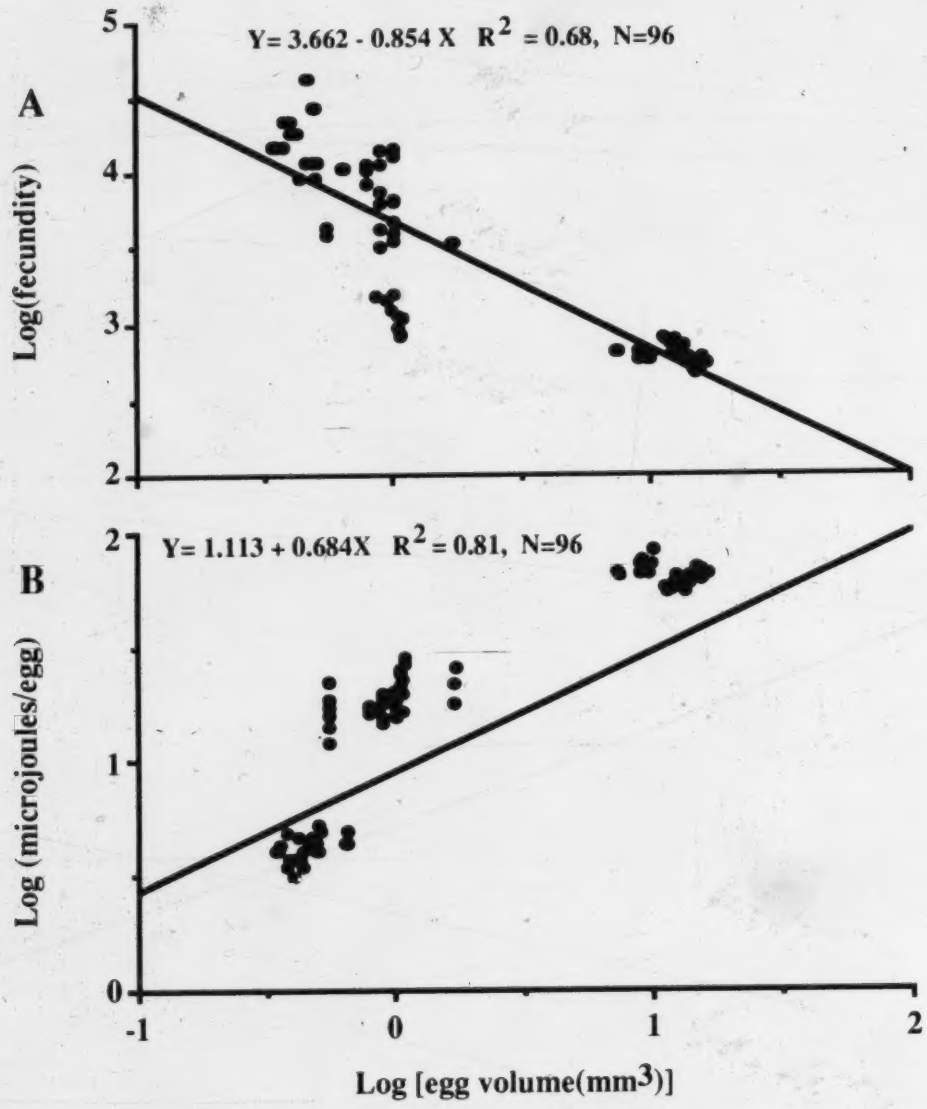

Figure III-2: Relationship between egg size and fecundity, and between egg size and energy content. Three clusters of plotted data represent three different developmental modes in *Capitella* sp.

(P>0.05 for each type). There was also an inverse relationship between egg size and fecundity (Fig. III-2B, P<0.001), but there was no relationship between egg size and fecundity within a single development type (P>0.05). Generally speaking, among three developmental modes, there is a trade-off between fecundity and egg size or between egg energy content (egg quality) and fecundity. Animals with the lowest fecundity (lecithotrophic developer) produced the largest eggs that contained the highest energy content, while animals with the highest fecundity (planktotrophic developers from squid egg capsules) produced the smallest eggs (Fig. III-2 A-B).

2. Reproductive effort and residual reproductive value

Reproductive effort was significantly different among three groups (One-way ANOVA: F=58.92, P<0.001); animals with lecithotrophic development had the lowest reproductive effort (41.5%) among the three groups, planktotrophic developers from subtidal squid egg capsules had the highest reproductive effort, whereas planktotrophic developers from intertidal area had an intermedian reproductive effort (Table III-2; T-test, P<0.01). Residual reproductive value of lecithotrophic developers was not significantly different from that of planktotrophic developers of squid egg capsule population (Table III-2; T-test: t=-1.77, P>0.05).

3. Effect of aging on reproductive characteristics of lecithotrophic developers

Out of fifty experimental worms, 43 individuals survived to the first spawn. The number of spawns per lifetime varied among individual worms. The mean number of spawns was 3.19 ± 0.95 times (range: 2-5 times) of 43 individuals. The interval between two successive spawns was about one month (s.d. ± 5 days).

Total fecundity (defined as the number of eggs produced in its life-time) also varied among the individuals observed. The average total fecundity was 2090 ± 792 (range: 398-3862) eggs/worm of 43 worms measured. With a hatching rate of 78.98 ± 11.53% (range: 56.2-95.1%) among 17 individuals (defined as the percentage of eggs in

Table III-2: Estimation of reproductive effort of *Capitella* sp. with different developmental models. Values are mean ± standard deviation (sample size). Here, reproductive effort = (energy in the eggs/total energy)*100%; residual reproductive value = (energy in the gonad/total energy)*100%.

	Lecithotrophic	Planktotrophic (subtidal)	Planktotrophic (intertidal)
Total energy (joules)	148.8±49.34 (51)	213.76±70.64 (17)	64.12±7.66 (22)
Joules in eggs	63.62±27.42 (51)	107.45±39.72 (17)	27.0±9.14 (22)
Joules in remaining gonad	35.32±13.88 (51)	55.03±42.92 (17)	----------
Joules in somatic tissue	49.87±11.82 (51)	51.28±14.20 (17)	37.14±6.20 (22)
Reproductive effort (%)	41.5±5.4 (51)	51.5±13.9 (17)	46.8±6.8 (22)
Residual reproductive value (%) (energy in remaining gonad/total energy)	23.6±4.1%	23.5±13.8% (17)	?

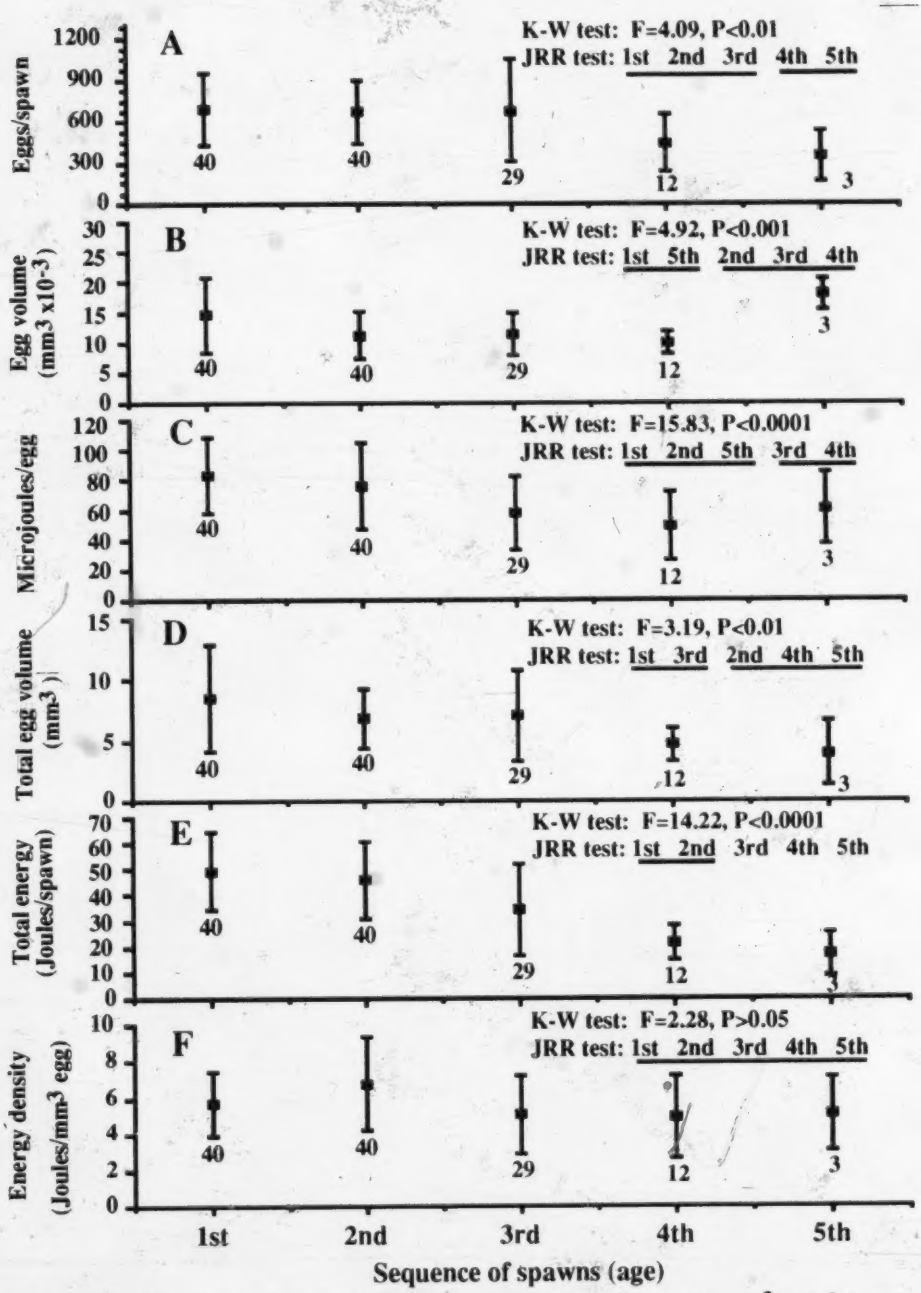

Figure III-3: Effects of aging on fecundity (A, eggs/spawn), egg size (B, $mm^3 * 10^{-3}$/egg), egg energy content (C, microjoules/egg), total egg volume (D, mm^3/eggs), total energy invested (E, joules in spawned eggs), and egg energy density (F) of *Capitella* sp. with lecithotrophic development. Values plotted are mean ± standard deviation with sample size below each bar. Results of Kruskal-Wallis test and Joint-Rank Ryan tests are also shown. Values not differing at 0.05 level are joined by a solid line.

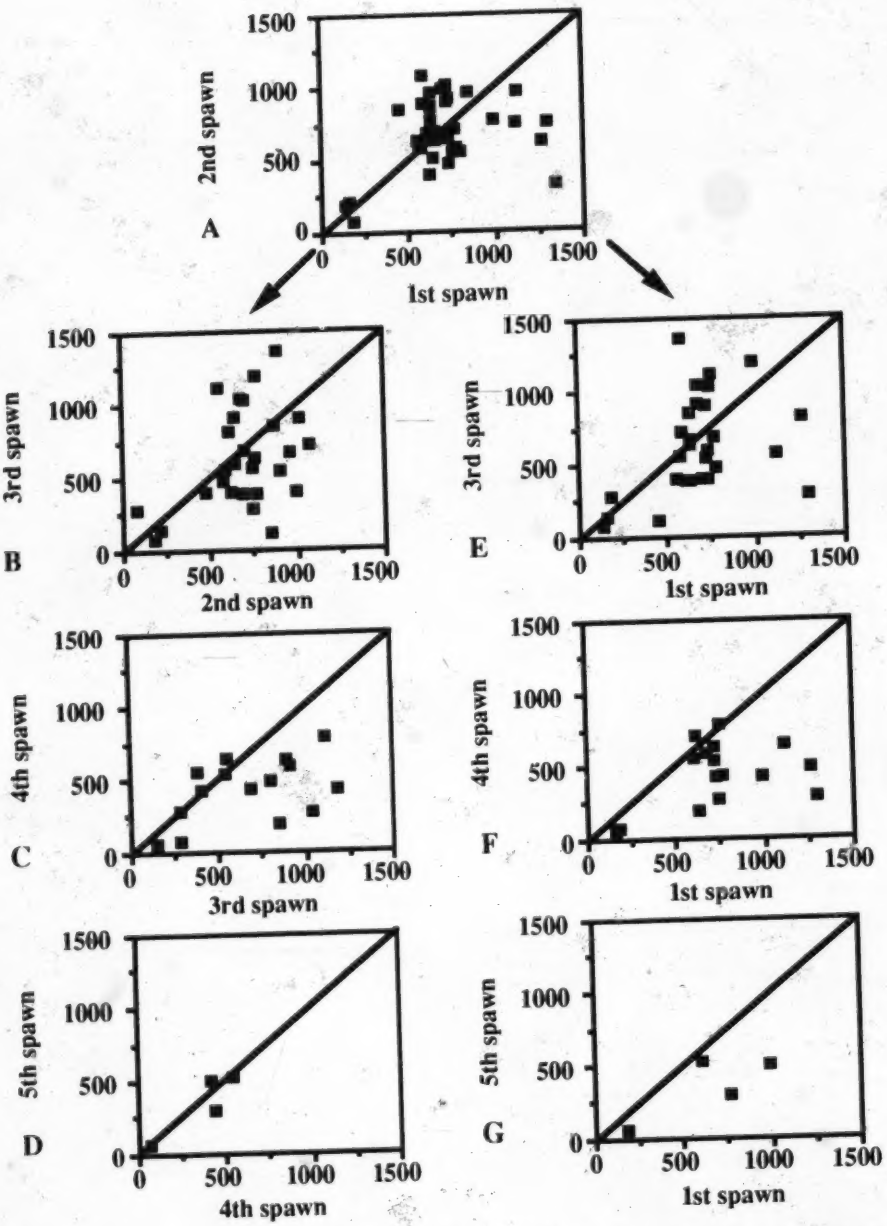

Figure III-4: Effect of aging on fecundity (number of eggs per spawn) of *Capitella* sp. with lecithotrophic development. Values plotted were the actual number of eggs produced by each worm in two spawns. Point on the diagonal line (zero-increase line) indicates that fecundities of the two spawns are identical. Fecundity favors "Y axis" if the point is above the diagonal line, and favors "X axis" if the point is below the diagonal line.

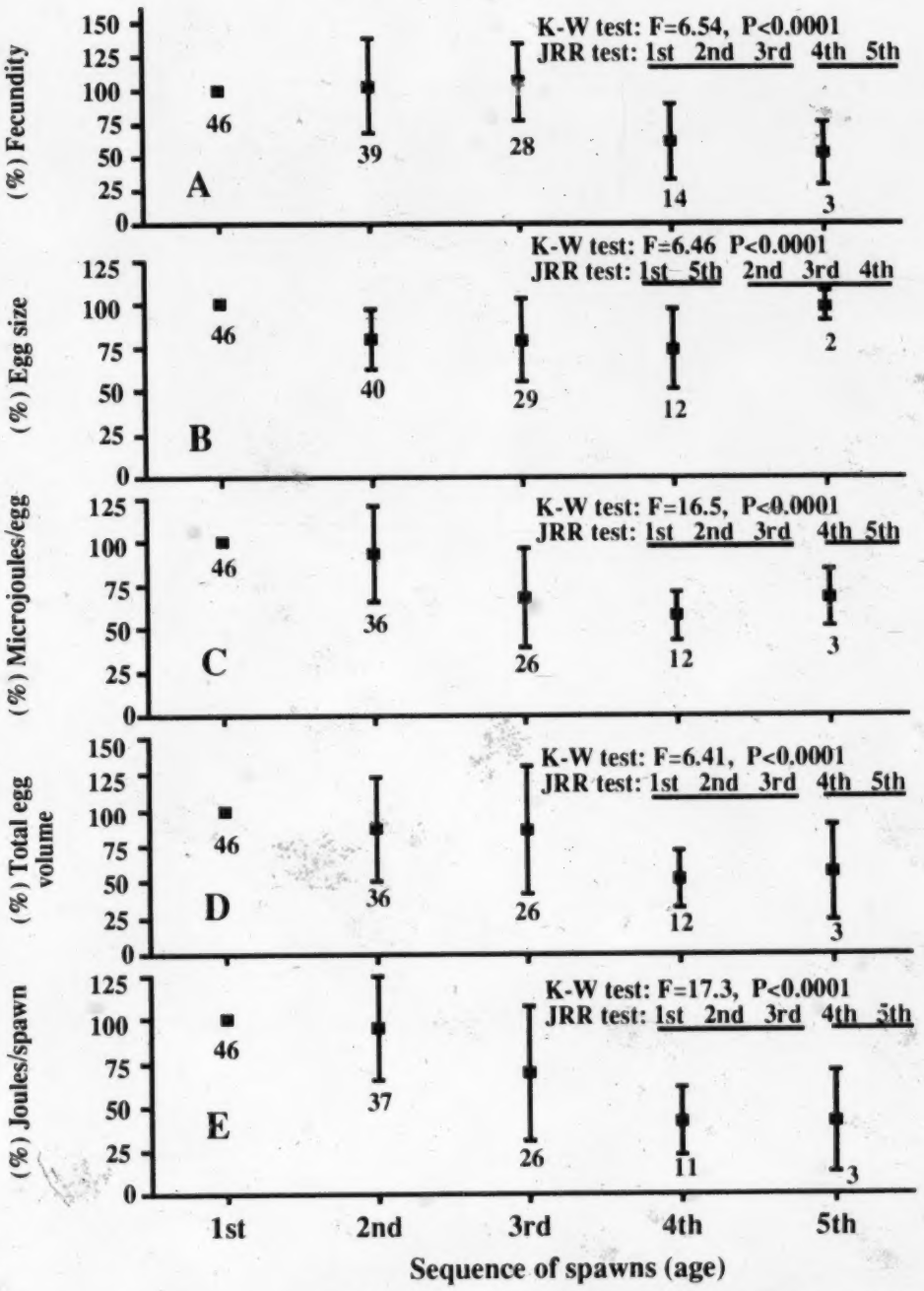

Figure III-5: The percentage of fecundity (A), egg size (B), egg energy content (C), total egg volume produced per spawn (D), and total energy invested in eggs per spawn (E) of *Capitella* sp. with lecithotrophic development. Values plotted are mean ± standard deviation with sample size below each bar. Results of Kruskal-Wallis test and Joint-Rank Ryan tests were also shown. Values not differing at 0.05 level are joined by a solid line.

Table III-3: Number of individuals of *Capitella* sp. that showed an increase (I) versus number of individuals showed a decrease (D) in one of five reproductive characteristics when the actual value of each reproductive characteristic in one spawn was compared with that in another spawn.

Parameter	2nd vs. 1st		3rd vs. 1st		4th vs. 1st		5th vs. 1st		3rd vs. 2nd		3rd vs. 4th		4th vs. 5th	
	I	D	I	D	I	D	I	D	I	D	I	D	I	D
Number of eggs	23	20	14	17	2	14	0	4	9	21	4	12	1	3
Egg size	6	34	4	25	1	11	1	1	10	17	2	9	2	0
Total egg volume	14	26	9	20	0	11	0	3	13	16	2	9	1	1
Egg energy content	10	30	4	25	0	12	0	3	6	23	4	8	2	1
Total energy/eggs	20	21	4	25	0	11	0	3	6	23	2	9	2	1

Table III-4: Summary of G-tests for null hypothesis that the number (p =0.5) of animals showing increase in each of reproductive characteristics is equal to that (q =0.5) of animals showing decrease when the values of two spawns were compared. Comparisons between the first and fifth spawns and between the fourth and fifth spawns were not conducted because of small sample sizes.

* indicates that null hypothesis was not rejected and number of individuals that showed significant decrease in reproductive parameter equals to that of those showing increase.

(§) indicates that the comparison was conducted with a chi-square test (with correction for continuity) rather than G-test.

Parameter	2nd vs. 1st		3rd vs. 1st		4th vs. 1st		3rd vs. 2nd		3rd vs. 4th	
	G	P	G	P	G	P	G	P	G	P
# of eggs	0.19	>0.50*	0.28	>0.50*	10.2	<0.005	4.98	<0.05	4.20	<0.05
Egg size	21.6	<0.001	16.9	<0.001	9.77	<0.005	1.86	>0.10*	4.82	<0.05
Total egg volume	3.72	<0.05	4.3	<0.05	9.1§	<0.005	1.68	>0.10	4.82	<0.05
Egg energy content	10.5	<0.001	16.9	<0.001	10.1§	<0.005	11.9	<0.001	1.36	>0.10*
Total energy/eggs	0.04	>0.75*	16.9	<0.001	9.1§	<0.005	11.9	<0.001	4.82	<0.05

the first spawn that finally developed into juveniles), one worm can produce approximately 1651 juveniles in its life-time. Total energy invested in the eggs by a worm throughout its lifetime was 131.57 ± 37.28 joules (range: 45.94-209.94 joules), and the total egg volume produced was 23.24 ± 8.19 mm^3 /female (range: 9.5-50.5).

The average fecundity (number of eggs per spawn) changed with age (Fig. III-3A). The JRR test detected that the average number of eggs produced in the first three consecutive spawns was not significantly different, but higher than those in the fourth and fifth spawns ($P<0.05$). Figure III-4 shows that a larger number of animals reduced the number of eggs in each consecutive spawns after the second spawn (Fig. III-4 A-D; Table III-3, III-4), whereas equal number of animals increased and decreased their fecundities in the second spawn (Fig. III-4 A-D; Table III-3, III-4). In general, more and more individuals showed decreased fecundity with aging (Fig. III-4 A-D). Compared with the first spawn, the proportion of individuals that increased the fecundity in either the second or third spawn was not significantly different from that of individuals showing a decrease, although almost all of individuals had much lower fecundity in the fourth and fifth spawn (Fig. III-4A, E-G; Table III-3,III-4). Also, in comparison with the first spawn, the proportional changes in fecundity were not significantly different in the first three spawns, but significantly lower in the fourth and fifth spawns (Fig. III-5).

Egg size decreased with age (Fig. III-3B). The JRR test revealed that the egg size in the second to fourth spawns was significantly smaller than that of the first spawn. An increase in egg size of the fifth spawn might be due to inadequate sample size. The changes in egg size over successive spawns might have been underestimated by combining data since large variation in egg sizes occurred among individuals. Figure III-6 shows that in general, the number of individuals that showed a decrease in egg size was significantly larger than that of individuals that showed an increase in egg size (Fig. III-6 A-D; Table III-3, III-4). Compared with the first spawn, a higher proportion of individuals produced smaller eggs in subsequent spawns (Fig. III-6A, E-G; Table III-

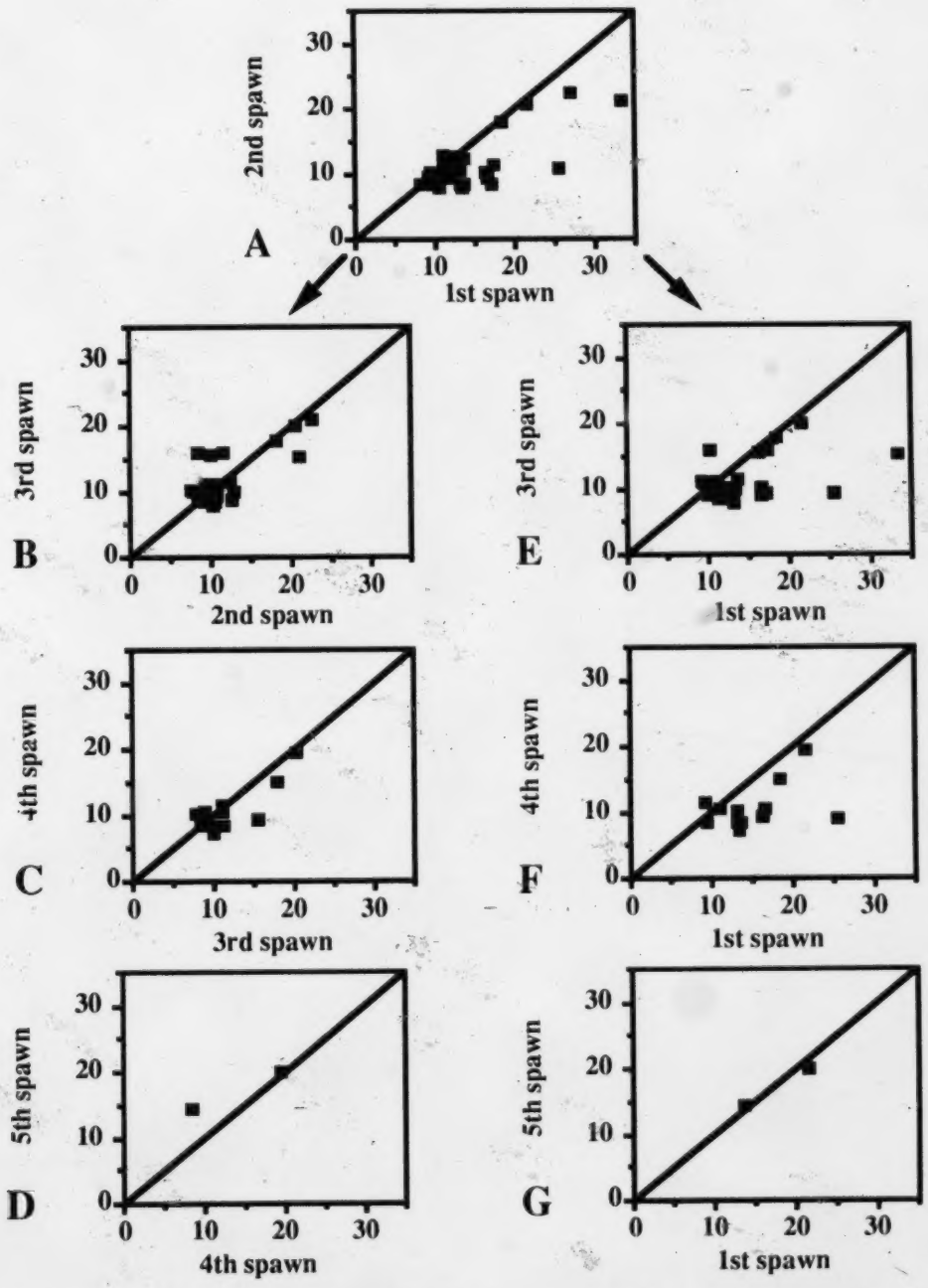

Figure III-6: Effect of aging on egg volume ($mm^3 * 10^{-3}$/egg) of *Capitella* sp. with lecithotrophic development. Values plotted were the mean egg size of each worm in two spawns. Point on the diagonal line (zero-increase line) indicates that egg sizes of the two spawns are identical. Egg size favors "Y" if the point is above the diagonal line, and favor "X" if the point is below the diagonal line.

3, III-4), where the egg size in the second to fourth spawns was about 70-80% of that in the first spawn (Fig. III-5).

Egg energy content was also affected by an animal's age (Fig. III-3C). The eggs produced in the first and second spawn contained more energy than those in the successive spawns (JRR test: $P<0.05$). Figure III-7 shows that a larger number of animals produced eggs that contained lower energy, as compared with the first spawn or with each of the consecutive spawns (Fig. III-7 A-D; Table III-3, III-4). Seventy-five per cent of animals showed a decrease in energy content/per egg for the second spawn, 86% in the third spawn and 100% in the fourth and fifth spawns (Figure III-7 A-G; Table III-3, Table III-4). Eggs produced by the same worm in the third or fourth spawn only contained about 57-67% energy produced in the first spawn (Fig. III-5).

The animal's age influenced the total egg volume per spawn (Fig.III-3D). The JRR test showed that the total egg volumes in the first and second spawns were significantly higher than those in the third to fifth spawns ($P<0.05$). Figure III-8 shows that a significantly larger number of animals had smaller total egg volumes with each of the next consecutive spawns (Fig. III-8 A-D; Table III-3, III-4), except in the second and third spawns, where the number of animals that increased or decreased total egg volume was not significantly different (Fig. III-8 A-D; Table III-3, III-4). In general, more and more individuals showed a trend of decreased total egg volume toward the later stages of life (Fig. III-8 A-D). Compared with the first spawn, a greater proportion of individuals produced a smaller volume of eggs in progressive spawns (Fig. III-8A, E-G; Table III-3, III-4). Total egg volumes in the second and third spawns were not significantly different from those in the first spawn, but those in the fourth and fifth spawns were only 50% of those in the first spawn (Fig. III-5).

Total energy content invested in the eggs decreased with an animal's age (Fig.III-3E) except for the first two spawns where total reproductive output was unchanged (JRR test: $P<0.05$). Figure III-9 shows that a significantly larger number of animals produced

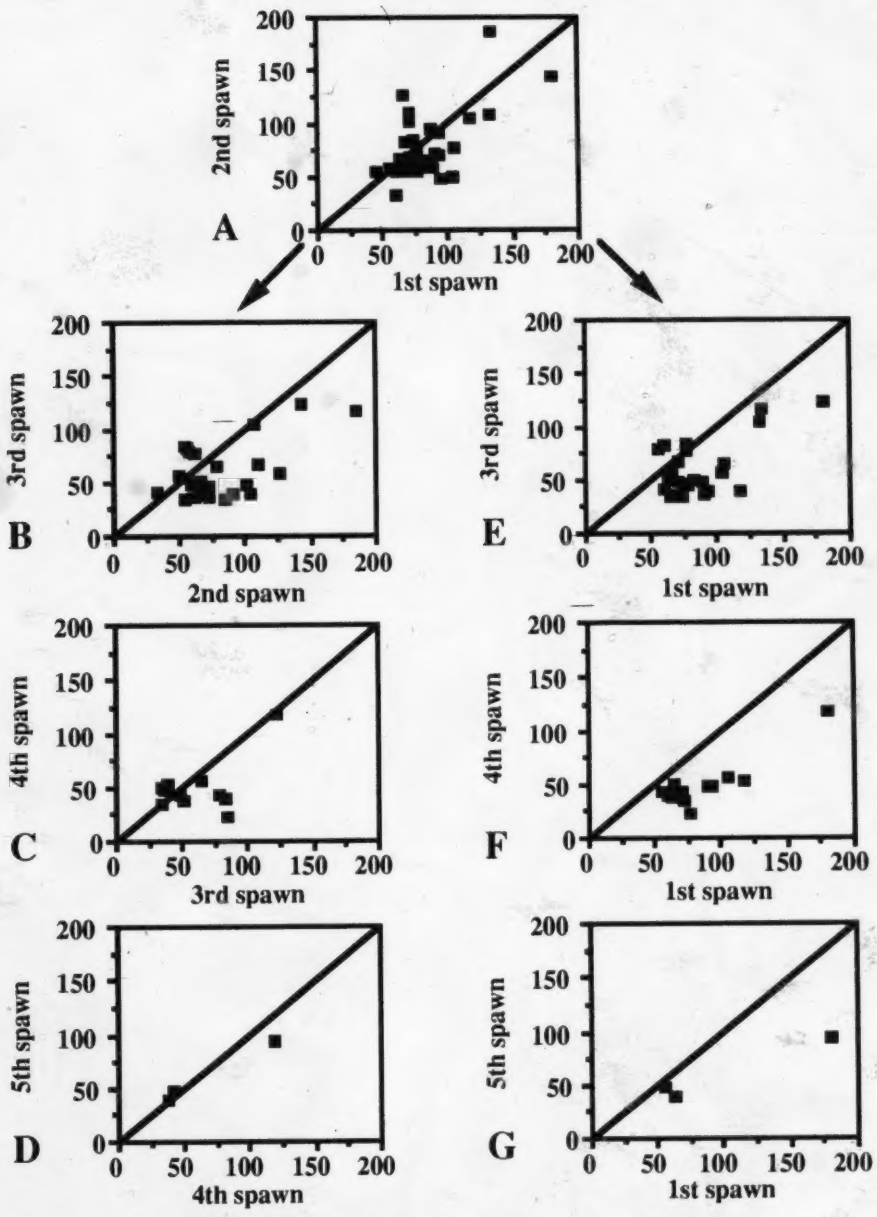

Figure III-7: Effect of aging on egg energy content (microjoules/egg) of *Capitella* sp. with lecithotrophic development. Values plotted were the egg energy content of each worm in two spawns. Point on the diagonal line (zero-increase line) indicates that egg energy contents of the two spawns are identical. Egg energy content favors "Y axis" if the point is above the diagonal line, and favors "X axis" if the point is below the diagonal line.

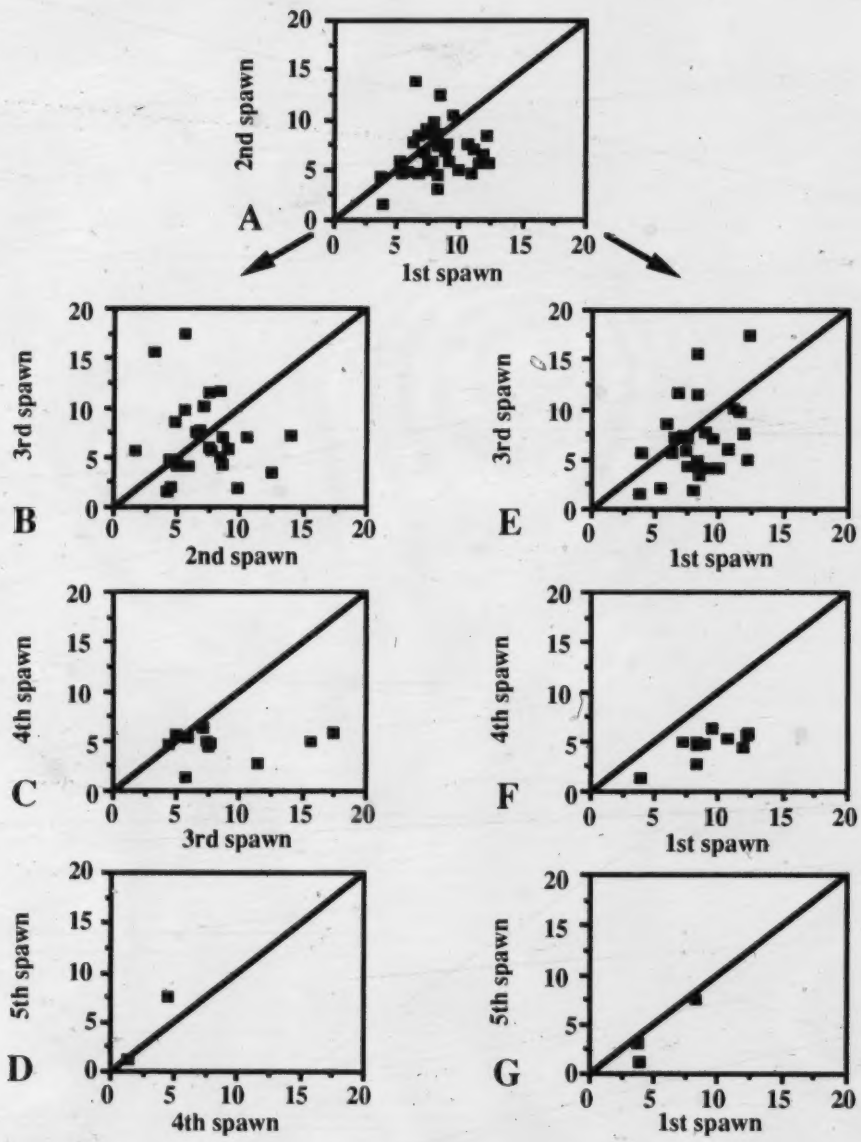

Figure III-8: Effect of aging on total egg volume (mm^3 /spawn) of *Capitella* sp. with lecithotrophic development. Values plotted were the total egg volume produced by each worm in two spawns. Point on the diagonal line (zero-increase line) indicates that total egg volumes of the two spawns are identical. Total egg volume favors "Y axis" if the point is above the diagonal line, and favors "X axis" if the point is below the diagonal line.

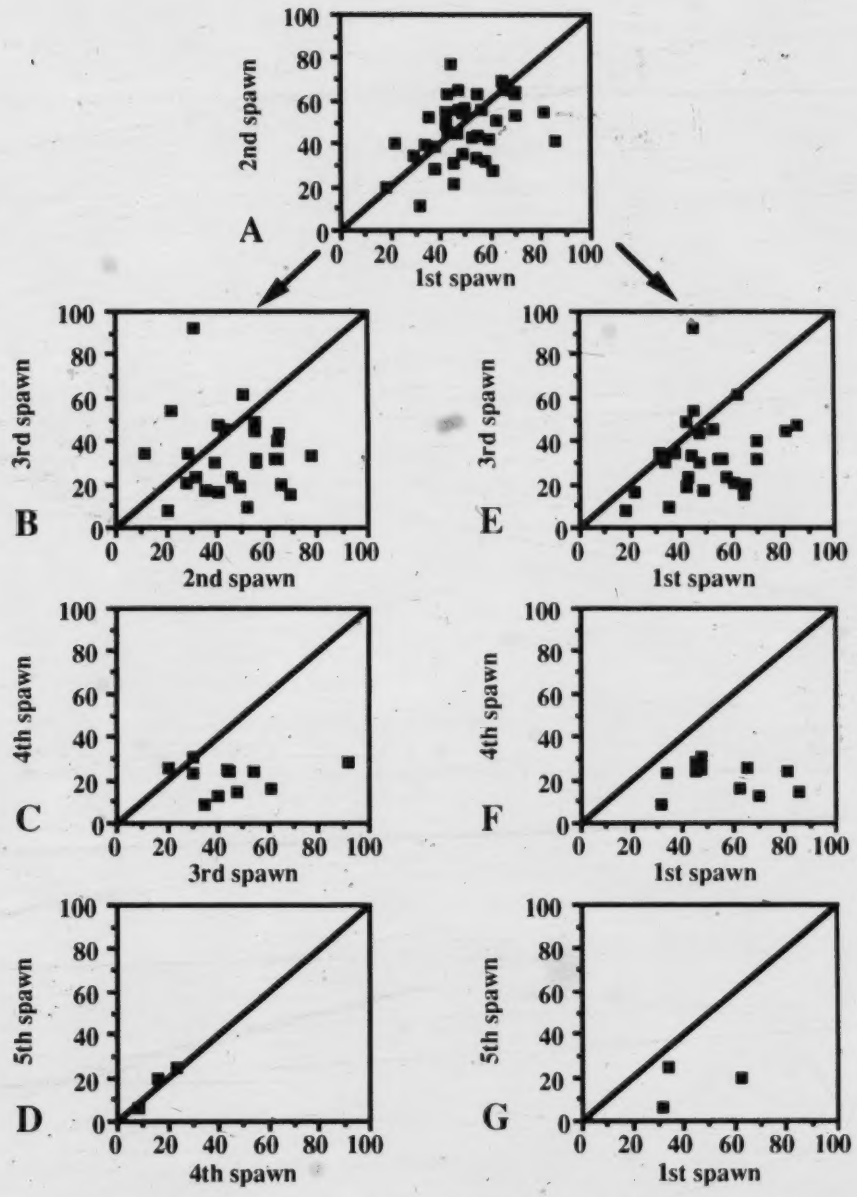

Figure III-9: Effect of aging on total energy invested in the eggs (joules/spawn) of *Capitella* sp. with lecithotrophic development. Values plotted were total egg energy content of each worm in two spawns. Point on the diagonal line (zero-increase line) indicates that total egg energy content of the two spawns are identical. Total egg energy content favors "Y axis" if the point is above the diagonal line, and favors "X axis" if the point is below the diagonal line.

eggs that contained lower energy when compared with the first spawn or with each of the consecutive spawns, except in the first and second spawns, where an equal proportion of animals showed a decrease and an increased in the total energy output in eggs (Fig. III-9 A-D; Table III-3, III-4). The energy invested in the eggs of the third spawn was about 69% of that in the first spawn, which declined to about 40% in the fourth and fifth spawns (Fig. III-5).

Figure III-3F indicates that aging had no effect on the energy density in the eggs, indicating that differences in egg energy content among spawns are mainly because of the differences in egg size.

4. Effect of aging on reproductive characteristics of planktotrophic developers

The number of spawns per life-time of the planktotrophic developers varied among individuals. On average, they spawned 2.6±1.0 times (range: 1-5). The interval between two successive spawns varied from two to five weeks. Total eggs produced in a lifetime also varied among 20 individuals, and average fecundity was 9458±4021 (range: 2025-16550) eggs/worm. Eggs/spawn was 3709±3414 (range: 821-11382) (14 times).

An animal's age influenced the number of eggs produced in each spawn (Fig. III-10A). In general, animal's fecundity increased in the first two spawns and then declined (Mann-Whiteney test: $U=1.0$, $P<0.01$).

Egg size and egg energy content varied with an animal's age (Fig. III-10B and III-10C). Animals produced larger eggs that contained more energy in the first spawn than in the second and third spawns (Mann-Whiteney test: $U=1.0$, $P<0.01$; $U=3$, $P<0.01$ for egg size and energy content respectively).

Total reproductive output in terms of total egg volume produced per spawn or total energy invested in eggs per spawn was not affected by an animal's age (Fig. III-10D and E).

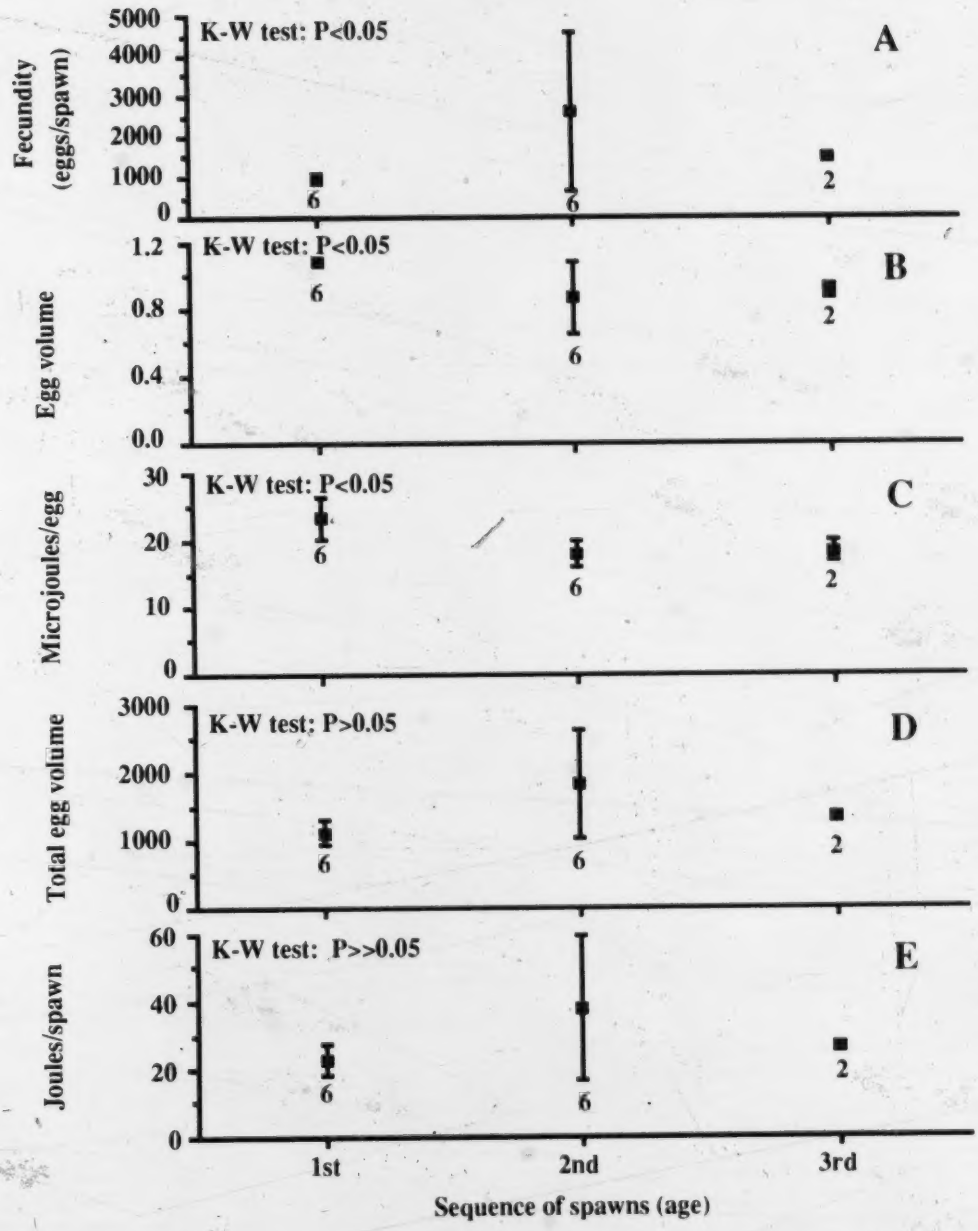

Figure III-10: Effects of aging on fecundity (A, eggs/spawn), egg size (B, $mm^3 * 10^3$ /egg), egg energy content (C, microjoules/egg), total egg volume (D, mm^3/eggs), and total energy invested (E, joules/spawned eggs) of *Capitella* sp. with planktotrophic development. Data plotted are mean ± standard deviation with sample size below each bar. Results of Kruskal-Wallis tests are also shown.

D. DISCUSSION

1. Relationship between reproductive effort and reproductive modes

Reproductive effort, ideally measured as the proportion of energy devoted by an organism to sexual reproduction, is a life-history characteristic that plays an important role in the analysis of life history strategies in marine invertebrates (Menge 1974, Stearns 1976, 1980, Hirshfield 1980, Grahame 1982, Thompson 1982, 1984, Tuomi *et al.* 1983, Grémare and Oliver 1986, Grémare *et al.* 1988). The theoretical prediction is that semelparous organisms should have higher reproductive efforts than iteroparous organisms (Gadgil and Bossert 1970, Hirshfield and Tinkle 1975). This prediction is correlated with the prediction that reproductive effort should increase as adult life expectancy decreases (Pianka 1976). Both predictions have been derived from the same assumption that there is a trade-off between reproductive effort and future life expectancy of the parent. Previous studies on reproductive effort, however, have yielded conflicting results. Some studies have demonstrated that animals with lecithotrophic development showed a greater reproductive effort (Menge 1974) while others have indicated that animals with planktotrophic development had a greater reproductive effort (Grahame 1977, Todd, 1979). Hughes and Roberts (1980) found that that there is no correlation between reproductive effort and reproductive modes in the order of Gastropoda. In this study, the results indicated that *Capitella* with lecithotrophic development showed a higher reproductive effort than those with planktotrophic development, which appears to support Menge's conclusion.

The measurement of reproductive effort poses problems because: 1) certain reproductive expenditures such as the energy devoted to care of the young, are difficult to measure, 2) the choice of index may critically alter the interpretation of data. For example, Grahame (1977) and Todd (1979) used the biomass of eggs compared with the biomass of parental somatic tissue while Thompson (1984) used the biomass of gametes

compared with the total biomass of somatic tissue and gametes. Attempts to compare the reproductive effort of animals from different taxa may have also led to confusion.

An increase in reproductive effort with advancing age appears to be the normal in many marine invertebrates and vertebrates investigated. For instance, in both oyster *Ostrea edulis* (Rodhouse 1978) and blue mussel *Mytilus edulis* (Thompson 1984), somatic production reaches an optimum in animals of intermediate age before declining in older individuals, whereas gamete production continues to increase. However, comparisons of reproductive effort per unit time as a function of age in different organisms will be complicated because of the differences in their physiological time scales (Hughes and Roberts 1980). In the present study, reproductive effort in the first spawn of three groups of *Capitella* were compared, thus, it may provide more reliable information.

It has been demonstrated in recent studies that reproductive effort can be highly variable between populations within a relatively small geographical region, whereas other parameters relating to reproductive strategy are more conservative (Bayne *et al.* 1983). It has also been suggested that reproductive effort is negatively correlated with the degree of stress (Bayne *et al.* 1983), which is consistent with Goodman's (1979) theoretical predictions. However, studies of a variety of organisms have demonstrated that enhanced reproductive effort (despite reduce fecundity) is a response to stress, especially a reduction in food ration (Gadgil and Bossert 1970, Hirshfield and Tinkle, 1975, Calow and Woodlhead 1977, Bayne *et al.* 1978, Thompson 1982). In this study, the results appeared to support the idea that animals have higher reproductive effort when they were under the pressure of food limitation. Animals collected from squid egg capsules have plentiful food that has high nutritional values while animals from intertidal mudflats that fed on detritus with poor nutritional values can be considered to be food-limited (see Chapter V). It was suggested here that differences in reproductive effort between planktotrophic developers from squid egg capsules and from intertidal mudflat were due

to the environmental differences.

2. Relationship between egg size and energy content

Many life-history strategy models have been based on assumption that the egg size is correlated to the energy content in the egg among the species (Vance 1973a, 1973b, Christiansen and Fenchel 1979, Pechenik 1979, Strathmann 1980, 1985). Although this relationship has been established among some echinoderm species (Strathmann and Vedder 1977, Turner and Lawrence 1979), recent studies have suggested that egg size may not be a reliable indicator of parental investment per offspring in intraspecific life history (McEdward and Carson 1987, McEdward and Coulter 1987).

In the present study, egg size was not correlated to egg energy content within each of three groups. However, there was a positive linear relationship among three groups; larger eggs contained more energy although the energy density of larger eggs was not significantly different from that of smaller eggs. Also, the largest egg contained the highest energy content and went through lecithotrophic development. This may suggest that the egg size could be used as an indicator of life-history strategy of the marine invertebrates if animals show fixed developmental modes.

3. Effect of aging on reproductive characteristics

It has always been difficult to study the effects of ages on reproductive characteristics of animals because of many practical problems. In birds and mammals for example, the techniques for marking and recapturing are so imperfect that recapturing rates are rarely high enough for quantitative analysis. It is even more difficult to mark and recapture marine invertebrates because techniques are poorly developed. Moreover, there are many environmental variables affecting reproductive characteristics of a species in the field. Therefore, even if mark and recapture techniques are successful for the animal under investigation, there still remains the problem of determining how many reproductive differences are because of the effects of age or environmental factors. For instance, although a recaptured organism in the second reproductive season may show

differences in its fecundity from the first year, this may be the result of a different physical and biotic environment that the animal has experienced to in different years. The differences in fecundity at the beginning and end of reproductive season may be due to variations in the animal's body size, temperature or food availability. Thus, the effects of age on fecundity, and between egg size and quality, can only be studied under controlled laboratory conditions, and with organisms that have a short life-span, a high growth rate and which can reproduce repeatedly.

In this study I have reported that age has effects on fecundity, egg size, egg energy content, total egg volume and total energy invested in the eggs in *Capitella* sp. Generally, all values for these features decreased with increasing age.

Although there is an increase in mean fecundity, egg size, egg energy content during the fifth spawn, I believe that these values were a consequence of sampling bias, because all the animals that lived to their the fifth spawn were individuals that had a lower fecundity, larger egg sizes, and higher egg energy contents than the rest of the animals in their first to fourth spawns. Averaged values based on information collected from these individuals were naturally much higher than those based on the entire group. The question as why those animals, which had lower fecundity and larger egg size, had a longer life-time and spawned more times than those who had higher fecundity and smaller egg size remains unanswered.

To avoid undue disturbance to the animals, I did not measure the changes of the body size of the experimental animals. Therefore, the relationship between body size and age was not studied. However, previously published data (Qian 1985) indicate *Capitella* reached their maximum body size prior to the first spawn. Subsequently, the animal size progressively decreased, and usually never recovered to the size of pre-spawning, and this appeared to be consistent with my current observation. Therefore, the lower fecundity and smaller egg size in older animals could be related to smaller body size.

Younger birds have been shown to lay smaller eggs in a number of species

(Brooke 1978, Crawford 1980, Gratto *et al.* 1983, Thomas 1983), and the same is true of some mammals (Sadleir 1969). It has been suggested that this is related to seasonal changes and may not have anything to do with age (see Sadleir 1969) . This study is the first attempt to determine variations in egg volume in consecutive spawns. The egg volume of lecithotrophic developers declined with consecutive spawns, namely, younger worms produced larger eggs. This finding differed from that of birds and mammals and rejected the hypothesis that the older individual compensate its lower fecundity by producing larger eggs so to increase the survival rate of the offspring.

There is information indicating that egg size and energy content are related to offspring survival, growth, life-span of larval stages, and development of post-larval stages (Kaplan 1980a, 1980b, Kaplan and Cooper 1984, Furness 1983, Duncan 1986, Kraeuter *et al.* 1986, Marsh 1984, 1986, Henrich 1988). However, there is not a single study that has successfully addressed the effect of animal's age on egg quality. In the present study, the results showed that both egg size and egg energy content decreased with age. This indicates that older individual not only produce fewer eggs but also produce eggs at poorer quality.

In both the oyster, *Ostrea edulis* (Rodhouse 1978), and blue mussel, *Mytilus edulis* (Thompson 1984), somatic production reaches an optimum in intermediate age before declining in older individuals, but gamete production continues to increase with age. Comparisons of reproductive effort per unit time as a function of age in different organisms , however, is complicated because of differences in their physiological time scales (Hughes and Roberts 1980). Therefore, the total reproductive output has been used as an indicator of reproductive success of marine invertebrates (Thompson 1984), and it appears that the reproductive output of animals increased immediately after reaching sexual maturity, reached its maximum in a short period, and then declined gradually with age. *Capitella* showed a similar tendency, although I did not measure the total reproductive effort. The reproductive output, in terms of total egg volume per spawn, did

not change much in the first three spawns, but declined rapidly thereafter. Total energy content in the eggs per spawn was not different in the first two spawns, but also dropped rapidly with age.

Judging from the available information, it appears that the age-based fecundity fluctuation observed in this study represents a uniform pattern. In all species investigated to date, there are apparently two main patterns. In three species tested, the maximum fecundity is found immediately after the beginning of the breeding season and then decreases gradually (Åkesson 1982, Levin *et al.* 1987, this study), whereas in other species the highest fecundity is found in the first spawn (Wu *et al.* 1987).

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CHAPTER IV

EFFECT OF FOOD QUANTITY ON EGESTION, GROWTH, AND REPRODUCTIVE CHARACTERISTICS

A. INTRODUCTION

Diet has been considered as one of the most important ecological components in determining the population dynamics of marine invertebrates. In most previous studies authors have examined the effects of diet on growth amongst marine invertebrates (Carefoot 1967, MacDonald and Thompson 1985a, 1986, Xu and Barker 1990, and many others) and less attention has been paid to the effects of diet on fecundity, egg size, egg energy content, and total reproductive output (Bayne 1975, Bayne *et al.* 1975, Levin, 1986, Levin and Creed 1986, Langton *et al.* 1987, Barber *et al.* 1988, Grémare, 1989a, 1989b, Hirche 1989).

Although it is possible that reproductive characteristics of a given species may not be affected by growth rate, I believe, however, that animals with a higher growth rate may either become larger at spawning or reach sexual maturity earlier than animals with a lower growth rate. Either of these two consequences will have important influences on the fitness of the individual. For instance, larger animals either release more eggs because of a positive correlation between body size and egg production (Petraitis 1985, and many others) or release larger eggs (better quality eggs) than smaller animals. In addition, larger eggs may result in offspring with better survival traits or a shorter larval life. Higher fecundity may give rise to a higher rate of recruitment in a population.

Among reproductive characteristics, egg size and egg quality are the most frequently used parameters in almost all the life-history models. Many previous studies have indicated that these characteristics are correlated with developmental mode, larval life-span, larval growth, mortality, and larval or juvenile sizes at hatching (Vance 1973a, 1973b, Kraeuter *et al.* 1982, Crump 1984, Marsh 1984, 1986). However, the relationships between egg size and the amount of food provided to adults, and between

egg quality and the amount of nutrients provided to the hatchling remain unclear. Chia (1974) suggested that marine invertebrates in nutrient-poor environments tend to produce fewer, but larger, eggs than those in nutrient-rich conditions. Although this hypothesis has not been tested properly among marine invertebrates, it appears to be true of many terrestrial animals.

This chapter is designed to examine the effects of food quantity on egestion rate, growth rate, generation time, fecundity, egg size, egg energy content, and larval development in *Capitella* sp. Previous studies have indicated that *Capitella capitata* occurs in high densities in heavily polluted areas (Grassle and Grassle 1974, Yamamoto 1980, Tsutsumi and Kikuchi 1983, Qian 1985, Wu and Qian 1987a, 1987b, Tsutsumi 1987; Wu *et al.* 1988), and population growth, individual growth, and reproductive output of this species are related to quantity and quality of food (Tenore 1975, 1977a, 1977b, 1981, Tenore *et al.* 1979, Tenore and Chesney 1985, Grémare *et al.* 1988, 1989a, 1989b). However, how food quantity affects ingestion rate of the animals on food (ingestion rate is indicated by egestion rate in this study) and in turn affects growth rate of animals has never been examined and, how the reproductive characteristics of *Capitella* (especially egg size and energy content) vary in response to food quantity remains unknown.

B. MATERIALS AND METHODS

1. Sediment treatment

The sediment used in all the experiments was obtained on August 17, 1987 from the intertidal mudflat at the head of Bamfield Inlet near the Bamfield Marine Station, British Columbia. Sediment was sieved through a 200 μm mesh, mixed thoroughly, and air-dried. Organic content of the sediment was approximately 8%, which was estimated from weight loss on ignition (475°C, 4h) after drying at 100°C for 24h.

2. Effect of food quantity and body size on egestion rate and fecal pellet weight

A two-way factorial design was used to test the effects of food rationing and animal size on fecal pellet size and egestion rate (in terms of weight and number of fecal pellets produced daily) of *Capitella*. The five food rations used in the experiments were as follows: 0.0, 1.0, 2.0, 3.0, 4.0 mg cereal (corn flakes, commercial products) per worm per day. The animals used were individuals from siblings of lecithotrophic developers. They were divided into the following five size classes: body volume = (1) 0.248 ± 0.056 mm^3; (2) 3.02 ± 0.66 mm^3; (3) 22.42 ± 2.84 mm^3; (4) 45.50 ± 11.92 mm^3; and (5) 134.74 ± 27.90 mm^3. Body sizes of these animals were determined by measuring 20 living worms of each size class. Each worm was rapidly transferred from a laboratory culture container to a glass Petri dish. After it was relaxed with 0.36M $MgCl_2$, body length (L) and body diameter (D) at the fifth setiger of each worm were measured under a dissecting microscope with the aid of an ocular micrometer. Finally, the body volume (V) of each individual was calculated according to the following equation: $\mathbf{V=\pi(D/2)^2L}$.

One hundred and fifty siblings of each size class were randomly selected and starved for 24 hours. These individuals were randomly assigned to 30 culture beakers (5 worms per beaker) that contained a 3 cm thick layer of treated sediment. The culture beakers were then randomly divided into 5 groups, each receiving food of a given ration (6 replicate beakers for each food ration). In total, 750 individuals and 150 experimental beakers were used in the experiments. After they had been allowed to feed for 24 hours at 10±1°C, the animals were removed from the beakers. The number of fecal pellets (larger than 53 μm) in each beaker was counted directly and was then divided by the number of the worms in that beaker to obtain egestion rate, which was recorded as fecal pellets/worm/day. Then, all the fecal pellets from each beaker were placed in a clean aluminium drying pan and dried in an oven at 100°C for 24 hours to obtain the dry weight

of the fecal pellets. Thus, egestion rates were also recorded as either fecal pellet dry weight/worm/day or fecal pellet dry weight/mm^3 body volume/day. Finally, the organic content of the fecal pellets and the sediment in each beaker were estimated from weight loss on ignition (475°C, 4h). It was found that the amount of organic content of both the fecal pellets and the sediment was close to 8%.

Two-way ANOVA tests were used to examine the effects of food quantity and animal size on egestion rate.

3. Food quantity on reproductive output, growth, and maturation

a. Experiment I:

Six hundred young juveniles from siblings (from planktotrophic development) of a single spawn were placed into 12 trays (15 x15 x 15 cm). Each tray had 50 µm mesh vents on each size and was provided with a 5 cm thick layer of treated sediment. The trays were randomly separated into four groups, each group receiving dried, ground *Ulva lactuca* at one of the following four rations: 5 mg, 1 mg, 0.1 mg, and 0.0 mg/worm/day (Fig. IV-1). The trays were provided with continuously flowing, 50 µm filtered seawater and submerged in a 12 cm deep seawater table. The temperature throughout the experiments was 10±1°C.

Prior to the addition of food, the dried, ground *Ulva* was soaked in seawater for 12 hours and then added to each tray. The sediment was replaced every two weeks. When the substratum was changed, the sediment and worms in each tray were gently transferred into a large dissecting pan. The number of living worms in each trays was counted under a magnifying glass at 2X to determine the survival rate, and all the animals were checked under a dissecting microscope to note the development of gonads. After the sediment had been replaced, the animals were returned to their original trays.

The developmental states of the gonads were arbitrarily determined by following the method described by Qian (1985). In brief, six stages were defined: **stage 0**, worms have no visible gonads (ovary); **stage 1**, worms have barely visible gonads; **stage 2**,

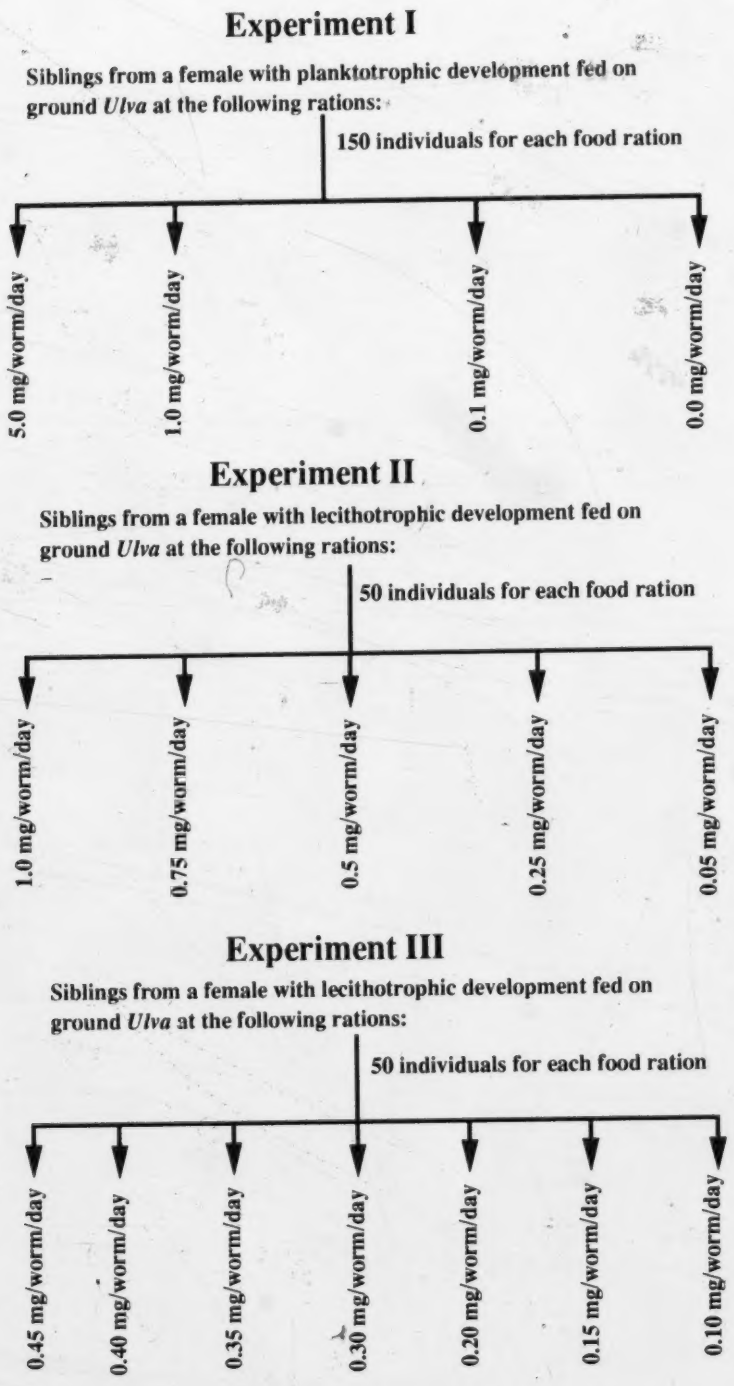
Experiment I
Siblings from a female with planktotrophic development fed on ground *Ulva* at the following rations:
150 individuals for each food ration
5.0 mg/worm/day
1.0 mg/worm/day
0.1 mg/worm/day
0.0 mg/worm/day
Experiment II
Siblings from a female with lecithotrophic development fed on ground *Ulva* at the following rations:
50 individuals for each food ration
1.0 mg/worm/day
0.75 mg/worm/day
0.5 mg/worm/day
0.25 mg/worm/day
0.05 mg/worm/day
Experiment III
Siblings from a female with lecithotrophic development fed on ground *Ulva* at the following rations:
50 individuals for each food ration
0.45 mg/worm/day
0.40 mg/worm/day
0.35 mg/worm/day
0.30 mg/worm/day
0.20 mg/worm/day
0.15 mg/worm/day
0.10 mg/worm/day

Figure IV-1: Outline of experimental design for experiments I, II, and III, assessing the effects of food quantity on growth and reproduction of *Capitella* sp.

worms have very-well developed gonads, but have no eggs in the coelom; **stage 3**, worms have a lot of eggs in the coelom; **stage 4**, worms with packed eggs in the coelom; and **stage 5**, worms are spent.

Growth rates were estimated by following the changes in the body length and the number of the setigers at two-week intervals from a subset of 5-10 animals of each replicate culture during 5 months. Animals were first relaxed in 0.36 M $MgCl_2$ and then measured under a dissecting microscope with the aid of an ocular micrometer. It is impossible to obtain the dry weight without sacrificing them. Wet weight was not used because gut contents can greatly affect the accuracy of the measurement.

When an animal began to release eggs in its tube, it was separated and placed in a small culture beaker. After it had released its last egg from the coelom into its tube, the worm was forced out of the tube. Then, the tube was gently opened with dissecting needles and the number of eggs was counted under a dissecting microscope.

After determining the fecundity of each reproductive individual, 20 or 30 eggs were randomly selected and mounted on a slide, and the long and short axes of each egg were measured under a compound microscope with the aid of an ocular micrometer. Egg volume (**V**) was calculated using the following equation: $\mathbf{V=(4/3)\pi A^2 B}$, where **A** and **B** are the length of short and long axes, respectively.

b. Experiment II:

Two hundred and fifty sibling juveniles (having lecithotrophic development) from a single spawn were cultured in 10 1-liter beakers. Beakers (each with a 5 cm layer of sediment) were divided into five pairs and each pair was given one of the five rations (quantity) of the dried food (ground *Ulva lactuca*): 1 mg, 0.75 mg, 0.5 mg, 0.25 mg, and 0.05 mg/worm/day (Fig. IV-1). Survival rate, growth rate, fecundity, and egg size were measured in the manner described in experiment I.

For each reproductive worm, three subsamples of 20 to 50 eggs were used to determine egg energy content. The measurement of energy content in the egg followed

the method outlined by Parsons *et al*. (1984) and McEdward (1986).

Total reproductive output was expressed by the total volume of eggs produced and by the total energy (J) invested in the eggs in the first spawn. These two values were calculated by multiplying the average egg volume or average egg energy content by fecundity.

Analyses of covariance (ANCOVAs) of the regression lines between survival and experimental times, and between growth (increases in the body length and the body volume) and experimental times of *Capitella* sp. were conducted to test the effect of food quantity on survivor and growth (Zar 1984). Where there was a significant difference in the slopes and elevations of those regression lines, Tukey multiple comparisons tests were used to examine the differences between lines. One-way ANOVAs and Student-Newman-Keuls multiple comparisons tests (Zar 1984) were used to test the effect of food quantity on spawning, fecundity, egg size, egg energy content, and total reproductive output.

c. Experiment III: response to changes in food quantity in sediment.

This experiment followed closely the procedures of experiment II. However, the focus on the animal's response to food quantity was under a narrow range of seven food rations: 0.45 mg, 0.40 mg, 0.35 mg, 0.30 mg, 0.20 mg, 0.15 mg, and 0.10 mg/worm/day (Fig. IV-1).

Three hundred and fifty sibling juveniles (having lecithotrophic development) were randomly divided into 14 beakers (25 worms/beaker), and cultures were maintained in the same way as in experiment II. Growth and fecundity were measured in the way described in experiment II.

In order to establish a relationship between fecundity and body size, each spent individual was removed from its tube and its body length, body width, body volume, and the number of setigers of the animal were measured in the manner described in experiment

I. Finally, the fecundity of each worm was plotted against its body size.

Data treatment and analysis were the same as those in experiment II.

C. RESULTS

1. Effect of food quantity and body size on egestion rates

Individual fecal pellet weight was affected by body size of experimental animals but not by food quantity (quantity) (Table IV-1). There was no significant interaction between animal size and food quantity (Table IV-1). Figure IV-2A shows the relationships between body size and fecal pellet size at five different food rations. Since food quantity did not affect the fecal pellet weight (Table VI-1, ANCOVA test, $P>0.05$ for both slopes and interceptions), the data for five food rations were pooled and plotted in Figure IV-2B, which indicates that larger animals produced heavier fecal pellets than did smaller animals (Figure IV-2B, $F=471.8$, $P<0.001$ for the regression line between body size and fecal pellet weight).

Food quantity and animal size had significant effects on the egestion rate of *Capitella*, with a significant interaction between food quantity and animal size (Fig. IV-3A; Table IV-2). The number of fecal pellets produced was positively related to the body sizes of the experimental animals; however, it was inversely related to food quantity for each size class (Fig. IV-3A). Within each food ration, the number of fecal pellets egested by the largest animals was about 8 times larger than that of the smallest individuals used in the experiment. Within each size class of the animals, the number of fecal pellets egested decreased with increasing food quantity, indicating that an animal under a low food regime processed a larger quantity of sediment than one under a high food regime.

Both body size and food quantity affected the body-volume specific egestion rate (reported as the number of pellets/mm^3 (body-volume)/day) of *Capitella* with a significant interaction between food quantity and body size (Table IV-2). Figure IV-3B shows that body-volume-specific egestion rate decreased exponentially with increasing

Table IV-1: The results of a two-way factorial ANOVA on the effects of body size and food quantity on fecal pellet size (dry weight) of *Capitella* sp. (from lecithotrophic development).

Source	DF	Sum of square	Mean squares	F	P
Food quantity	4	4.75	1.19	0.42	0.80
Size class	4	5225.1	1306.3	459.1	<0.001
Interaction	16	59.86	3.74	1.32	0.23
Error	50	142.3	2.85		
Total	74	5432.0			

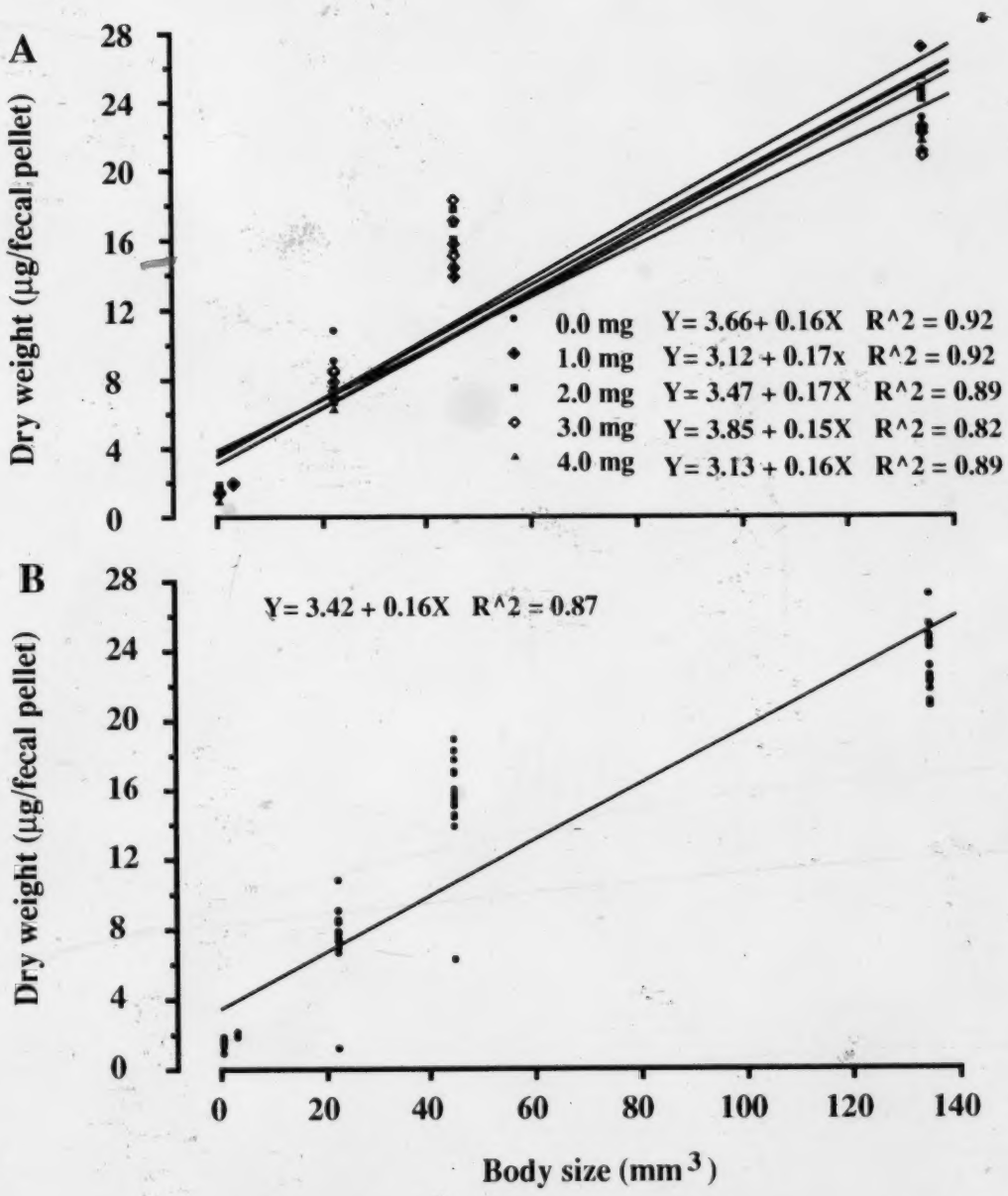

Figure IV-2: Relationship between animal size and dry weight of egested fecal pellet of *Capitella* sp. (from lecithotrophic development). A, regression lines between animal size and fecal pellet weight at each of five food rations (0.0, 1.0, 2.0, 3.0, and 4.0 mg/worm/day); B, regression line between animal size and fecal pellet weight. The body volume given is the mean value of 20 animals measured at the beginning of the experiment.

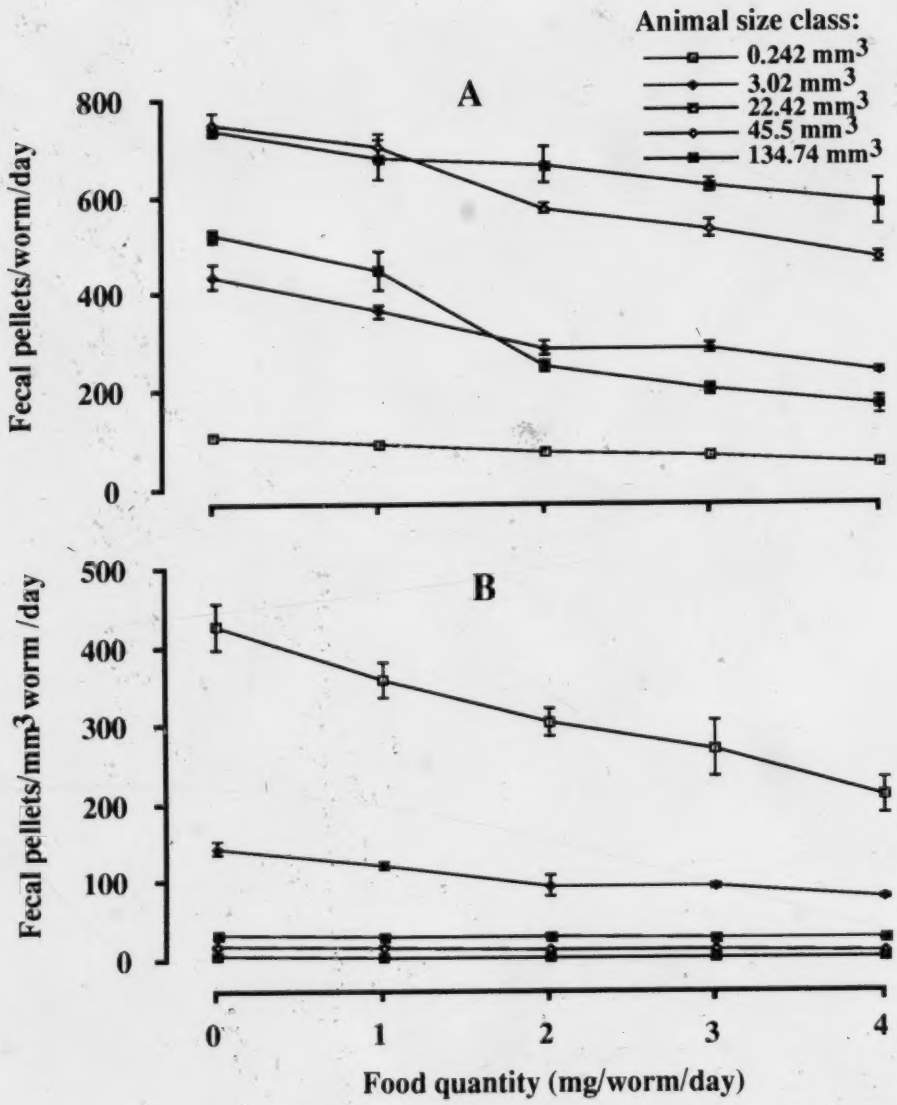

Figure IV-3: Effects of food quantity and body size on fecal pellet production of *Capitella* sp.(from lecithotrophic development). The size of each size class given is the mean value of 20 animals measured at the beginning of the experiment. Values plotted are mean ± standard deviation of six replicates. A, fecal pellets/worm/day; B, fecal pellets/mm^3 body volume/day.

Table IV-2: The results of two-way factorial ANOVA on the effects of body size and food quantity on egestion rates of *Capitella* sp. (from lecithotrophic development).

Source	DF	Sum of square	Mean squares	F	P
		Number of feces/worm/day			
Food quantity	4	430771	107692.9	212.1	<0.001
Size class	4	3361591	840397.8	1655.1	<0.001
Interaction	16	142106	8944.1	17.6	<0.001
Error	50	25388	507.8		
		Number of feces/mm^3 worm/day			
Food quantity	4	31636	7909.1	49.0	<0.01
Size class	4	1004470	251117.6	1554.3	<0.001
Interaction	16	59880	3742.5	23.2	<0.001
Error	50	8078	161.6		
		mg feces (dry weight)/worm/day			
Food quantity	4	93.8	23.5	79.4	<0.01
Size class	4	1035.5	258.9	876.5	<0.001
Interaction	16	122.9	7.7	11.8	<0.001
Error	50	14.8	0.3		
		mg feces (dry weight)/mm^3 worm /day			
Food quantity	4	0.253	0.063	65.9	<0.01
Size class	4	2.884	0.721	751.3	<0.001
Interaction	16	0.181	0.011	11.8	<0.001
Error	50	0.048	0.001		

body size and with increasing food quantity.

Both body size and food quantity also affected the dry weight of the total fecal pellets egested daily by a single individual, with a significant interaction between food quantity and body size (Table IV-2). The amount of feces egested increased with increasing body size within each food ration but decreased with increasing food quantity within each size class (Fig. IV-4A).

Fecal pellet dry weight/mm^3 worm was reversely correlated with the body size and also decreased with the food quantity (Fig. IV-4B, Table IV-2).

2. Effect of food quantity on growth, maturation, and reproductive output

a. Experiment I

Food quantity affected survival rate (Fig. IV-5, Table IV-3), as animals fed at 5.0 and 1.0 mg rations had higher survival rates than those fed at rations of 0.0 and 0.1 mg/worm/day. A Tukey multiple comparisons test (Tukey test) indicates that animals fed at 5.0 and 1.0 rations had similar survival rates, whereas animals fed at 0.1 and 0.0 (starved) rations had similar survival rates. On average, 77.3% and 69% animals remained by the end of four month experiments at 5.0 and 1.0 rations, respectively, compared with 48.7% at 0.0 ration and 32.0% at 0.1 mg ration.

Food quantity had a great effect on growth rate. Figure IV-6 shows the changes in the body length and the number of setigers over the experimental times at the four food rations. Animals fed at 5.0 and 1.0 mg/worm/day had a similar growth rate (in terms of increasing in the body length), which is higher than that of animals fed at 0.1 mg/worm/day or that animals starved (Fig. IV-6A, Table IV-4). Within 4 months, the animals at 5.0 and 1.0 mg ration reached to an average length of 55-60 mm long, whereas the animals at 0.1 mg food ration only grew to a size of 27.7 mm long and those starved grew to 19.5 mm long. A Tukey test ranked the animals' growth rate as follows in a decline order: 5.0 mg/worm/day = 1.0 mg/worm/day >> 0.1 mg/worm/day > 0.0 mg/worm/day.

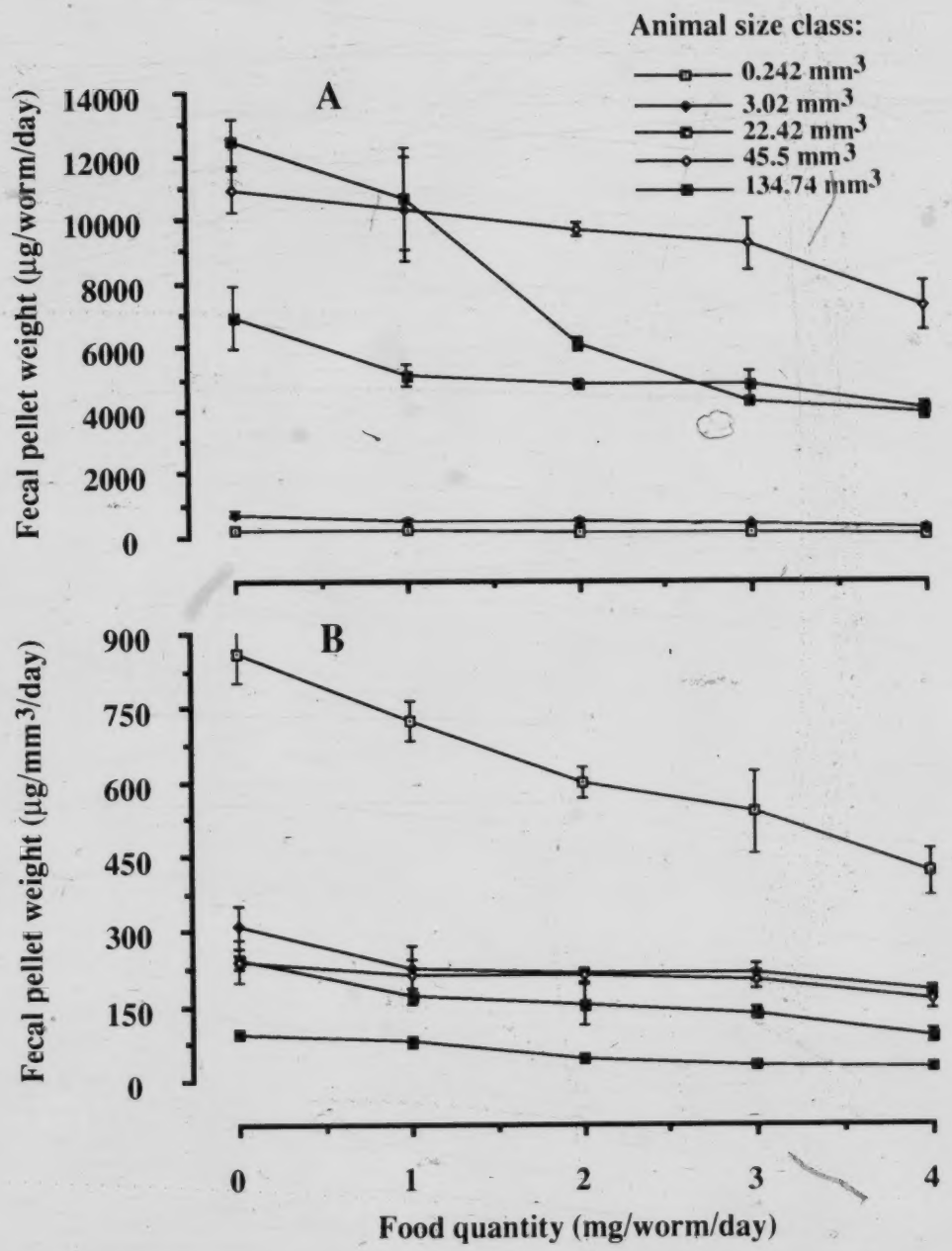

Figure IV-4: Effects of food quantity and body size on fecal pellet production of *Capitella* sp. (from lecithotrophic development). The size for each class given is the mean value of 20 animals measured at the beginning of the experiment. Values are mean ± standard deviation of six replicates. A, Dry weight of fecal pellets (µg/worm/day); B, Dry weight of fecal pellets (µg/mm^3 /day).

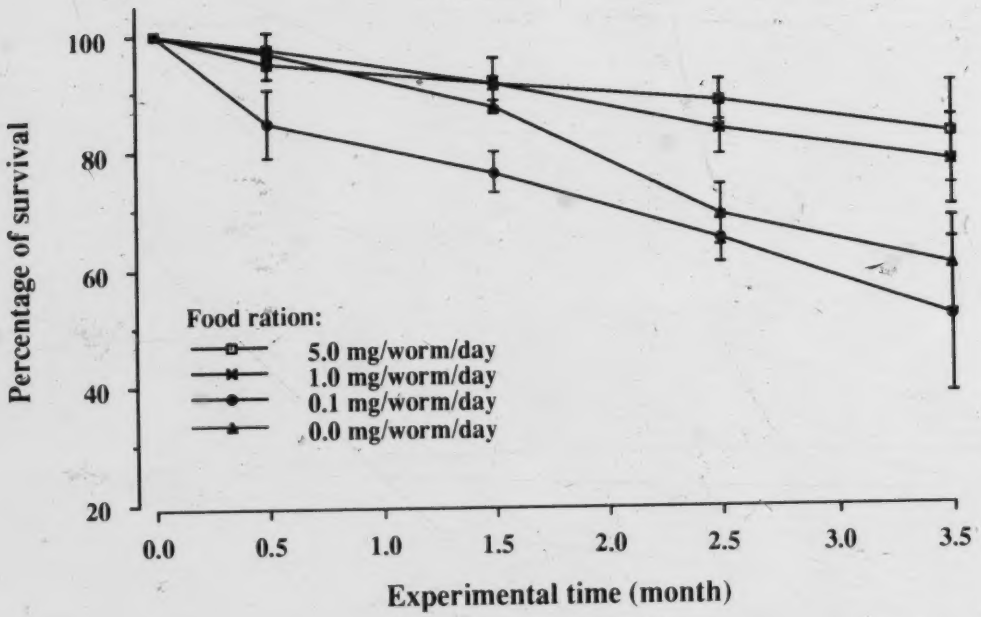

Figure IV-5: Effect of food quantity on survival rates of *Capitella* sp. (from planaktotrophic development). Data plotted are mean ± standard deviation of three replicate cultures.

Table IV-3: Least square linear regression equations of survival rate over 3.5 months of *Capitella* sp. (from planktotrophic development) fed at different food rations. Results of an ANCOVA are also shown.

	Regression			ANCOVA			
Food ration (mg/worm/day)	Regression equation	df	r^2		df	F	P
5.0	Y=99.8 - 5.02 X	4	0.99	Slope	3, 12	12.12	>0.05
1.0	Y=99.4 - 6.28 X	4	0.99	Elevation	3, 15	15.25	<0.05
0.1	Y=95.8 - 12.81 X	4	0.97				
0.0	Y=101.9 - 12.11X	4	0.98				

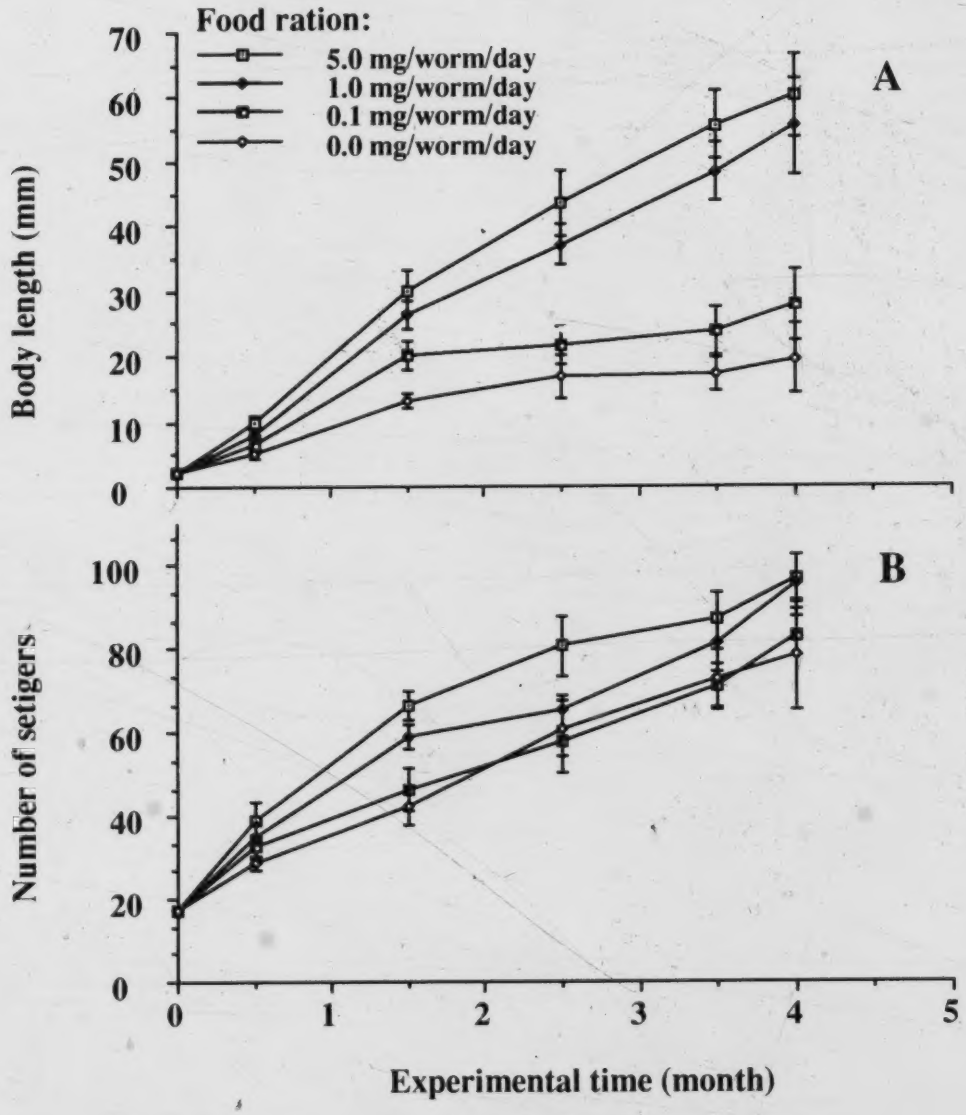

Figure IV-6: Effect of food quantity on growth of *Capitella* sp. (from planktotrophic development). Data plotted are mean ± standard deviation from measurement of 15 animals. A, body length; B, number of setigers.

Table IV-4: Least square linear regression equations on the changes in average body length and average number of setigers over 4 months of *Capitella* sp. (from planktotrophic development) fed at different food rations. Results of an ANCOVA are also shown.

Food ration (mg/worm/day)	Regression			ANCOVA			
	Regression equation	df	r^2		df	F	P
	Body length (mm)						
5.0	Y=4.06 + 14.7 X	4	0.99	Slope	3, 12	27.95	<0.05
1.0	Y=2.98 + 13.3 X	4	0.99	Elevation	3, 15	13.59	<0.01
0.1	Y=5.0 + 6.0 X	4	0.89				
0.0	Y=3.87 + 4.2 X	4	0.92				
	Number of setigers						
5.0	Y=27.6 + 18.4 X	4	0.93	Slope	3, 12	1.17	>0.05
1.0	Y=23.4 + 17.8 X	4	0.96	Elevation	3, 15	20.57	<0.01
0.1	Y=21.3 + 15.0 X	4	0.98				
0.0	Y=19.4 + 15.3X	4	0.99				

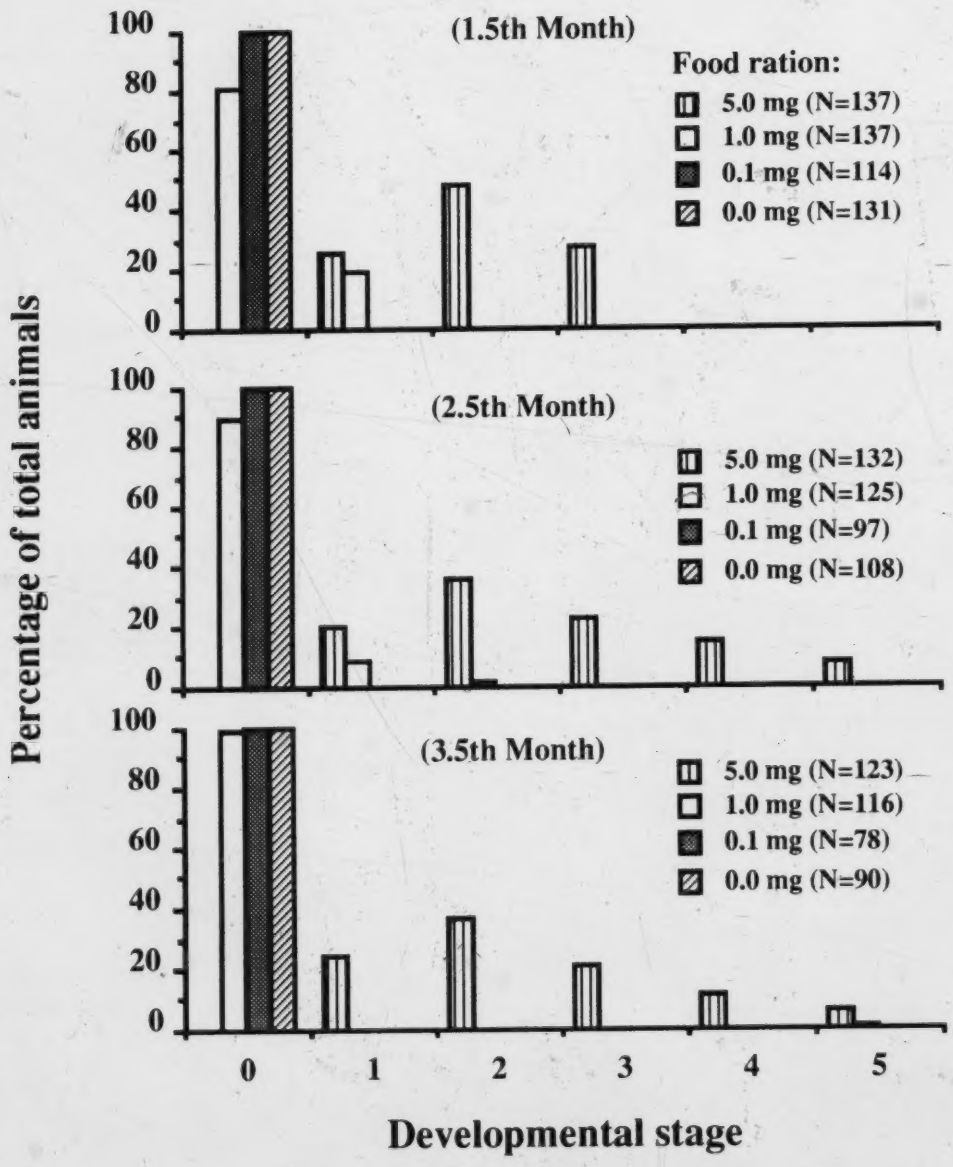

Figure IV-7: Effect of food quantity on sexual maturity of *Capitella* sp. (from planktotrophic development). Data plotted are proportional animals at a given developmental stage of gametogenesis, which were defined as follows: Stage 0, without visible ovary; Stage 1, barely visible ovary ; Stage 2, well developed ovary, no eggs in the coelom; Stage 3, some eggs in the coelom; Stage 4, coelom packed with eggs, ready to spawn; Stage 5, post-spawned worm.

The increase of setigers was also influenced by food quantity (Fig. IV-6B, Table IV-4). Within the first three months, the effects of food quantity on the increase of the number of setigers were significant, but were diminished at the later stages of the experiments (after 3.5 months). By 4.5 months, the animals in the 4 groups had a similar number of setigers although their body sizes were significantly different.

Food quantity affected gonadal development and sexual maturity (Fig. IV-7). In the 5 mg/worm/day ration group, some animals reached sexual maturity within two months, with a generation time of about 2 months. Only 7 out of 110 individuals in the 1.0 mg/worm/day ration reached sexual maturity by the end of four months. No individuals from 0.1 and 0.0 mg/worm/day rations developed visible gonads within the same period (4 months).

In the 5 mg/worm/day ration group, 75% of the reproductive females produced planktotrophic larvae, and 25% produced lecithotrophic larvae. In the 1.0 mg/worm/day ration group, all reproductive females produced lecithotrophic larvae. The fecundity and egg size of the animals that produced lecithotrophic larvae in both groups were not significantly different (t-test:$P>0.5$).

The mean fecundity of the animals that produced planktotrophic larvae (A: 9761±935, N=13) was higher than that (614±103, N=7) of the animals that produced lecithotrophic larvae. The animals with lecithotrophic development produced larger eggs ($\bar{X}$=284.9±17.0, N=1040), where the animals with planktotrophic larvae produced smaller eggs (122.9±16.2, N=1080).

When food is limited, animals appeared to spend all their energy on growth (1.0 mg/worm/ day ration produces body size similar to 5.0 mg/worm/ day ration).

After 4 months, the animals from group with 0.1-0.0 mg/worm/day ration were supplied with abundant food and they all developed gonads and began to reproduce within one month after the introduction of food.

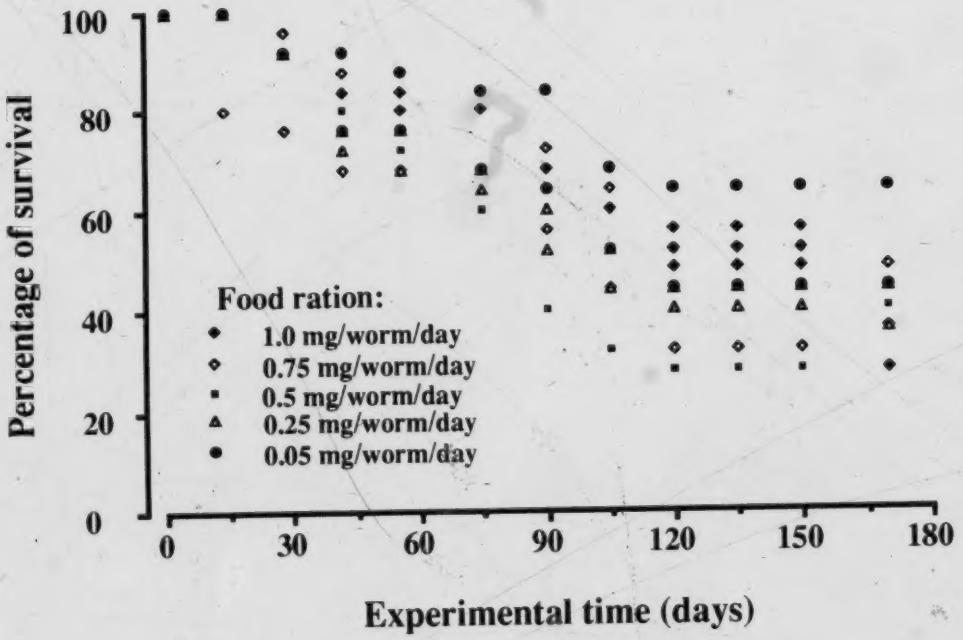

Figure IV-8: Effect of food quantity on survival rates of *Capitella* sp. (from lecithotrophic development).

Table IV-5: Least square linear regression equations on survival rate over 5.5 months of *Capitella* sp. (from lecithotrophic development) fed at different food rations. Results of an ANCOVA are also shown.

Food ration	Regression			ANCOVA			
(mg/worm/day)	Regression equation	df	r^2		df	F	P
1.0	Y=102.4 - 0.36 X	11	0.95	Slope	4, 50	2.22	>0.05
0.75	Y=97.2 - 0.38 X	11	0.80	Elevation	4, 54	9.28	<0.05
0.5	Y=98.6 - 0.44 X	11	0.84				
0.25	Y=97.5 - 0.40 X	11	0.91				
0.05	Y=99.8 - 0.32 X	11	0.78				

b. Experiment II:

Food quantity affected the survivorship of *Capitella* sp. (from lecithotrophic development) (Fig.IV-8, Table 5). Animals fed at 1.0 and 0.05 mg rations had better survival rate than those fed at the other three food rations (Tukey test, $P<0.05$).

Food quantity affected animal' growth, with higher food rations producing greater growth rates (in both body volume and body length) (Fig. IV-9A and B, Table IV-6). The average body volume of the sexually matured animals fed at 0.75 mg/worm/day was 157% of that of animals fed at 0.05 mg ration. Animals fed at 1.0 mg ration, however, had a lower growth rate than that of animals fed at 0.75 mg ration. This was mainly because animals fed at 1.0 mg ration had a lower growth rate at an early stage, where an excess amount of food left in the culture tray within each sampling interval reduced oxygen level and produced extremely high concentrations of hydrogen sulphide in the sediment.

Food quantity affected the timing of breeding (Fig. IV-10, Table IV-7). Animals fed at 0.5 mg ration were the first to spawn among the five groups, while those fed at 0.75 mg ration were second (Tukey test, $P<0.05$). By day 218 of the experiments, 121% of animals fed at 0.5 mg ration had spawned, whereas only about 50-63% of the animals on other rations had spawned. As more than 100% at 0.5 mg ration had spawned, this indicates that some of the individuals in this group had spawned twice during this period. It should be noted that Figure IV-10 did not include data from the 1.0 mg ration, this was because all animals in that group died shortly after spawning had begun.

Food quantity influenced the number of the eggs (fecundity) of the first spawn, as fecundity increased with increasing food quantity except of animals fed at 1.0 mg ration (Fig. IV-11A, Table IV-8). A lower fecundity at 1.0 mg ration, in part, was related to smaller adult sizes when compared with that at 0.5 mg ration. Animals fed at 0.05 mg ration produced an average of 367 eggs, compared with 1032 eggs for animals fed at 0.75 mg ration.

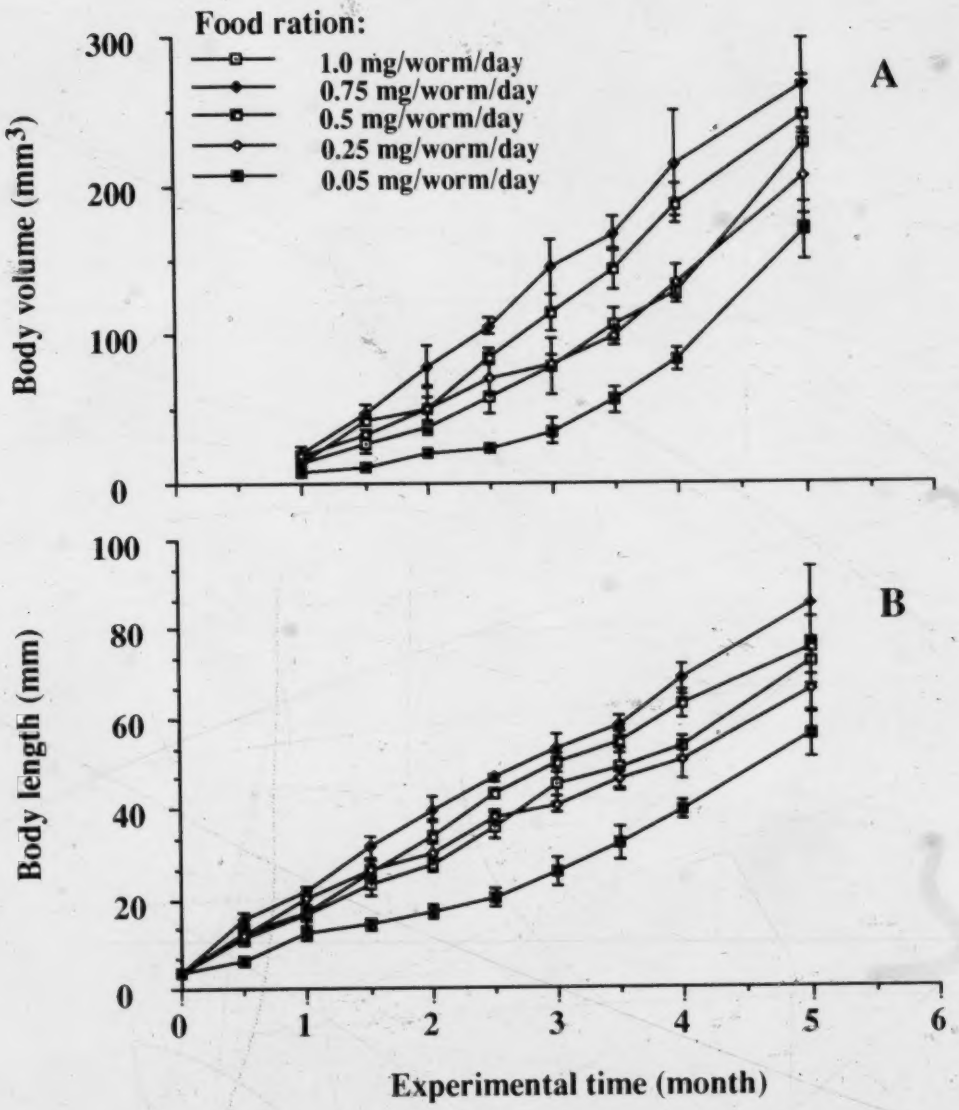

Figure IV-9: Effects of food quantity on growth of *Capitella* sp. (from lecithotrophic development). Data plotted are mean ± standard deviation from measurement of 15 animals. A, body Volume; B, body length.

Table IV-6. Least square linear regression equations on the changes in average body length and average body volume over 5 months of *Capitella* sp. (from lecithotrophic development) fed at different food rations. Results of an ANCOVA are also shown.

Food ration (mg/worm/day)	Regression			ANCOVA			
	Regression equation	df	r^2		df	F	P
	Body length (mm)						
1.0	Y=3.52 + 13.2 X	9	0.994	Slope	4, 35	5.58	>0.05
0.75	Y=6.33 + 15.7 X	9	0.996	Elevation	4, 39	28.6	<0.01
0.5	Y=4.40 + 14.6 X	9	0.997				
0.25	Y=6.66 + 11.6 X	9	0.989				
0.05	Y=0.10 + 9.87 X	9	0.953				
	Body Volume (mm3)						
1.0	Y=-57.0 + 50.4 X	7	0.929	Slope	4, 30	5.30	>0.05
0.75	Y=-47.0 + 63.1 X	7	0.996	Elevation	4, 34	18.1	<0.01
0.5	Y=-56.0 + 59.2 X	7	0.986				
0.25	Y=-38.2 + 44.4 X	7	0.95				
0.05	Y=-53.6 + 37.1 X	7	0.834				

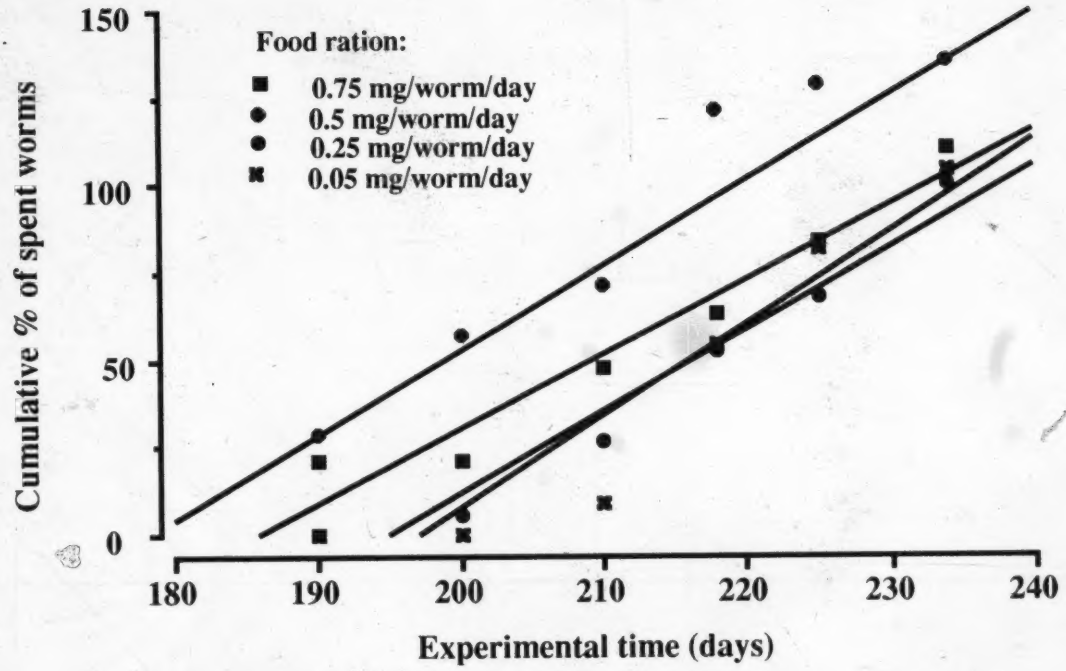

Figure IV-10: Effect of food quantity on breeding of *Capitella* sp. (from lecithotrophic development). Data plotted are cumulative percentages of animals spawned at each food ration.

Table IV-7: Least square linear regression equations on the cumulative percentage of spawned individuals over two reproductive months of *Capitella* sp. (from lecithotrophic development) fed at different food rations. Results of an ANCOVA are also shown.

Food ration (mg/worm/day)	Regression			ANCOVA			
	Regression equation	df	r^2		df	F	P
0.75	Y=-395.1 + 2.13 X	5	0.95	Slope	3, 16	0.53	>0.05
0.5	Y=-471.1 + 2.64 X	5	0.94	Elevation	3, 19	22.56	<0.05
0.25	Y=-455.4 + 2.34 X	5	0.96				
0.05	Y=-518.4 + 2.63 X	5	0.89				

Egg size and food quantity were inversely related. Animals fed at a higher food ration had a higher fecundity, but produced smaller eggs than those fed at a low food ration (Fig. IV-11B, Table IV-8). A SNK test indicates that animals fed at 0.05-0.50 mg rations produced larger eggs than those fed at 0.75 and 1.0 mg/worm/day (Fig. IV-11B, Table IV-8).

Energy content of the egg was affected by food quantity. Larger eggs produced by animals fed at lower food rations contained more energy (Fig. IV-11C, Table IV-8). It is interesting that the eggs produced by the animals at 0.5 mg ration contained the highest amount of energy (100.3 microjoules/egg), although the average egg size of this group was intermediate. Difference between the highest and lowest energy content among the five experimental groups is about 150% (100.3 microjoules at 0.5 mg ration versus 70.7 microjoules at 1.0 mg ration).

Total reproductive output was significantly affected by food quantity among the five groups. Figure IV-11D shows the total egg volume per spawn (Fig.IV-11D; Table IV-8). Animals fed at 0.5 mg ration produced 2.4 times of the egg volume as compared to those at 0.05 mg ration. Total energy invested in the eggs per spawn was also affected by food ration (Fig. IV-11E; Table IV-8). A SNK test indicates that amount of energy invested in the eggs are significantly different among the 5 groups, although there was no linear relationship between total energy invested in the eggs per spawn and food ration. Animals fed at 0.5 mg ration invested more than 2.6 times of energy than those fed at 0.05 ration. There was no significant differences in egg energy density (microjoules/mm^3 egg) among the five groups (Fig. IV-11F; ANOVA, $P>0.05$).

c. Experiment III: response to changes of food quantity in sediment.

Poor food supply did not appear to have definitive affects on the mortality of the animals. Within the range of 0.1 to 0.45 mg rations, food quantity did not affect the survivorship of the animals.

Table IV-8: The results of one-way ANOVA and Student-Newman-Keuls multiple comparisons test on reproductive characteristics of *Capitella* sp.(from lecithotrophic development) fed at five food rations (0.05, 0.25, 0.5, 0.75, 1.0 mg/worm/day). Values that did not differ at the 0.05 significant level are joined by a solid line. Values of all parameters are shown in ascending rank order from left to right.

Parameters	One-way ANOVA				SNK-test
	MS	df	F	P	(food ration)
Eggs/brood	1440509	4, 80	176.0	<0.0001	0.05 0.25 1.0 0.5 0.75
Egg size (mm^3/egg)	8.31	4, 59	3.82	<0.01	1.0 0.75 0.5 0.25 0.05
Total egg volume	153925490	4, 59	103.3	<0.0001	0.05 0.25 1.0 0.5 0.75
Microjoules/egg	36.25	4, 133	14.9	<0.0001	1.0 0.75 0.25 0.05 0.5
Joules/spawned eggs	9563463	4, 137	143.7	<0.0001	0.05 0.25 1.0 0.5 0.75

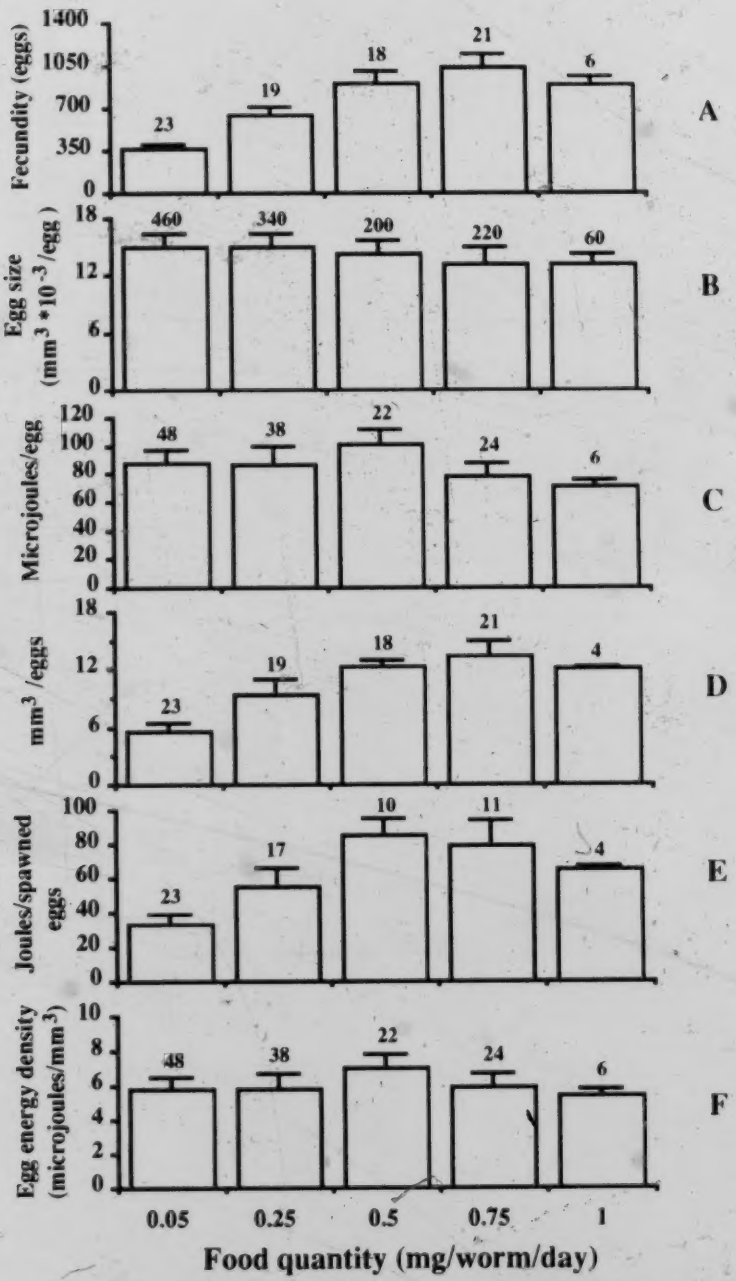

Figure IV-11: Effects of food quantity on reproductive characteristics of *Capitella* sp. (from lecithotrophic development). Data plotted are means ± standard deviation with sample size on the top of each bar. A, fecundity; B, egg size; C, egg energy content; D, total egg volume/spawn; E, total energy invested in spawned eggs; and F, egg energy density .

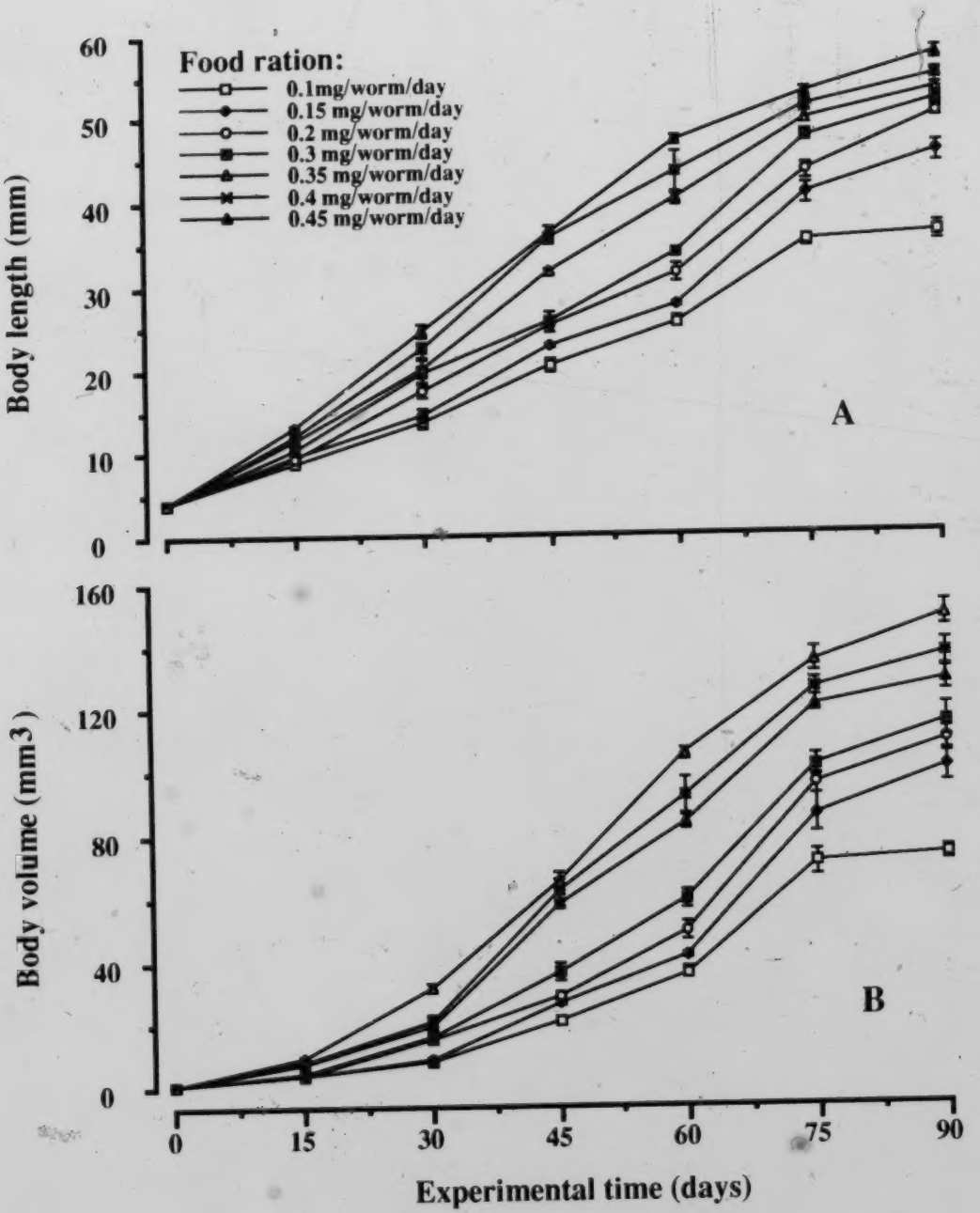

Figure IV-12: Effects of food quantity on growth of *Capitella* sp. (from lecithotrophic development). Datat plotted are mean ± standard error from measurement of 10 animals. A, the changes in body length; B, the changes in body volume.

Food quantity within the tested range of these experiments affected the body volume and the body length of the sexually matured animals (Fig. IV-12A and B; Anova:F=61.3, P<0.001; F=88.5, P<0.001 for body length and body volume, respectively, N=133). Figure IV-12 shows that within the first 3 months after the experiments had begun, animal body lengths and body volume increased rapidly with the growth curves fitting a linear regression line very well. After 3 months, growth slowed, possibly because of the onset of gametogenesis. Body size (both body length and body volume) at the spawning time were positively correlated with food quantity (Fig. IV-13 A-B). At spawning time, average body volume of the individuals fed at 0.45 mg ration was 324.5 mm^3 which was 219% of that (147.5 mm^3) of the individuals fed at 0.10 mg ration. Animals fed at 0.45 mg ration measured 81.5 mm in body length, whereas those fed on 0.1 mg ration measured 48.9 mm long.

A striking finding was that at the food regimes tested, food quantity did not affect the sexual maturity of lecithotrophic developers; all animals in each group almost released their eggs within 2 weeks after the first individual had spawned, even though they had different body sizes.

As predicted, minor changes in food quantity significantly affected the animal's fecundity. Figure IV-14 shows that there is a linear relationship between food quantity and the number of eggs produced of the first spawn (Anova: F=103.4, P<0.001, df: 6, 123; Table IV-9).

Higher fecundity of animals fed at a higher food ration can be attributable to their larger body size, since there was a distinctive relationship between body length and fecundity (Fig. IV-15A; Anova: F=244.5,P<0.001) Fecundity was also related to body volume of the breeding individuals (Fig. IV-15B; Anova: F=278.6, P<0.001) when data from all groups were pooled, even though there was no relationship between fecundity and body size (in terms of body volume or body length) within each group. In addition, the total reproductive output (total volume or energy content of the eggs), was not related

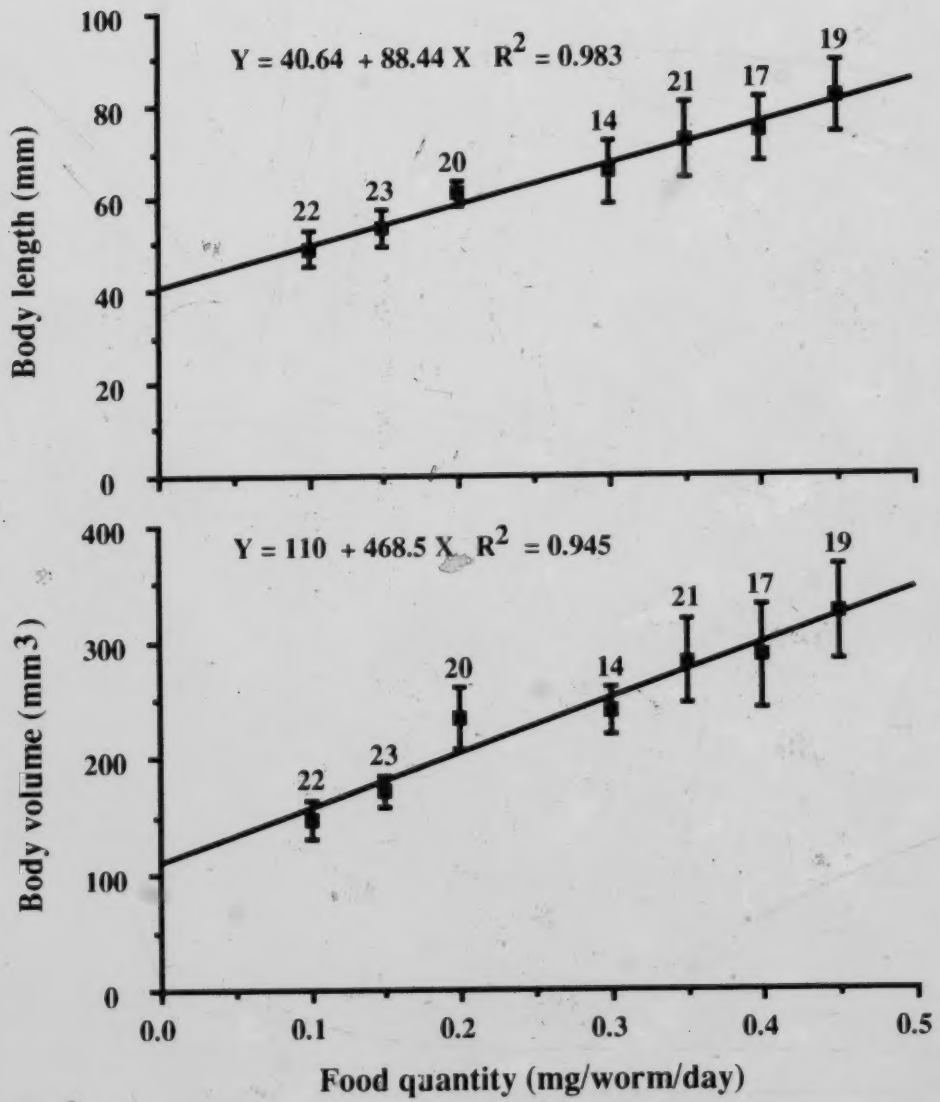

Figure IV-13: Effect of food quantity on body size at spawning of *Capitella* sp. (from lecithotrophic development). Data plotted are mean ± standard deviation with the sample size on the top of each bar. A, body length; B, body volume.

Table IV-9: The results of Student-Newman-Keuls multiple comparisons test on the fecundity (eggs/1st spawn) of *Capitella* sp. (from lecithotrophic development) among the seven food rations (0.1, 0.15, 0.2, 0.3, 0.35, 0.4, 0.45 mg/ind./day). x and N. S. indicate that values did or did not differ significantly at the 0.05 significant level respectively.

Fecundity (eggs/spawn)								
	Food ration	0.1	0.15	0.2	0.3	0.35	0.4	0.45
438.8	0.1							
482.5	0.15	x						
583.4	0.20	x	x					
629.0	0.30	x	x	N.S.				
695.2	0.35	x	x	x	x			
712.4	0.4	x	x	x	x	N.S.		
913.7	0.45	x	x	x	x	x	x	

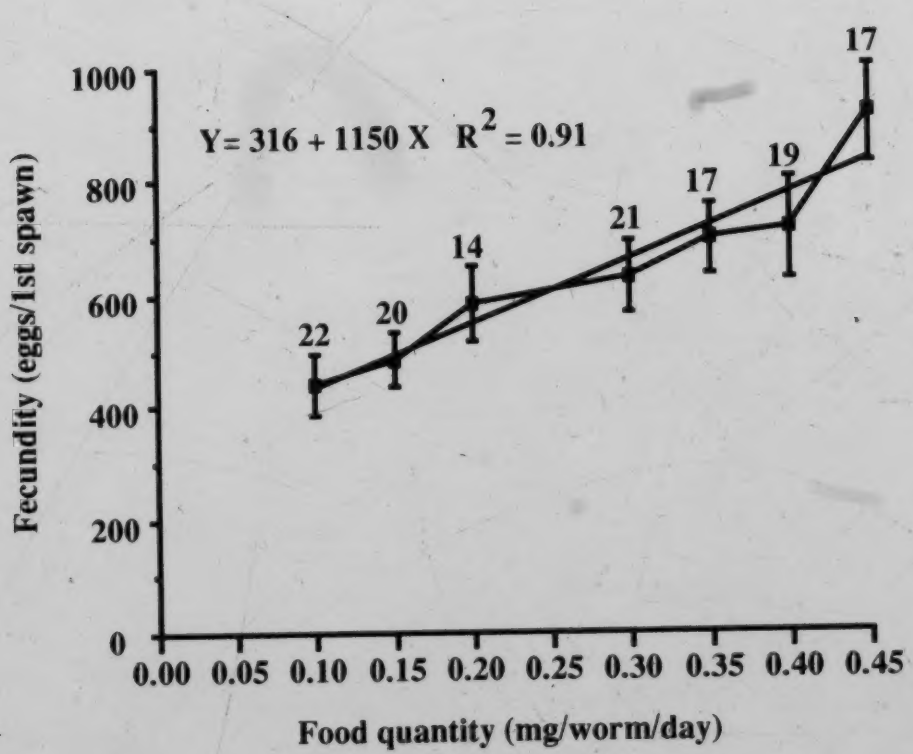

Figure IV-14: Effects of food quantity on fecundity of *Capitella* sp. (from lecithotrophic development). Data plotted are mean ± standard deviation with sample size on the top of each bar.

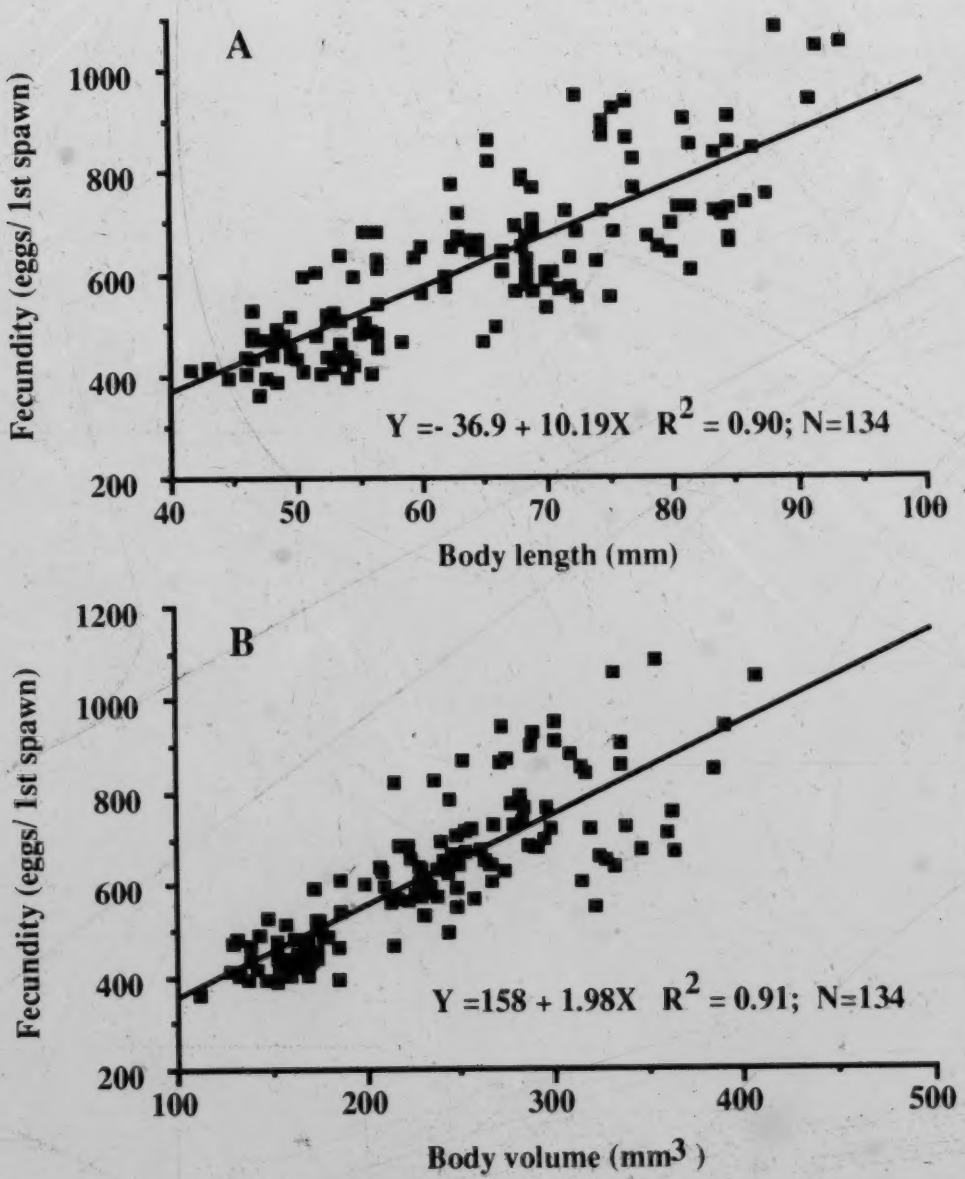

Figure IV-15: Relationship between body size and fecundity of *Capitella* sp. (from lecithotrophic development). Animal size was measured from individual that have just released all eggs into its tube. Fecundity was defined as the number of eggs deposited by a individual in its first spawn. A, body length vs. fecundity; B, body volume vs. fecundity.

to the body volume.

After pooling data on the effect of food quantity on fecundity from experiment II and III (Fig. IV-16), it was found that food quantity showed even stronger affects on animal fecundity as the significance level of Anova test increased by one order (ANOVA test: $F=138.33$, $P<0.0001$). A SNK test shows that the fecundities of the animals that were fed at different food rations were ranked as follows: 0.05mg < 0.01mg = 0.15mg < 0.2mg = 0.25mg = 0.3mg < 0.35mg = 0.4mg < 0.45 = 0.5mg = 1.0mg < 0.75mg.

D. DISCUSSION

1. Egestion rate and body size

Forbes and Lopez (1987) reported that egestion rate in *Capitella* sp I is related to body size by an allometric exponent less than one. This relationship was corroborated by my experimental results because the weight-specific production rate of *Capitella* sp. decreased exponentially or linearly with body size. Forbes and Lopez (1987) explained that changes in specific feeding rate that are related to body size occur due to: (1) fecal pellet production rate remains unchanged as a function of body size, and (2) smaller animals produce relatively heavier pellets. They concluded that worms control egestion rate without changing pellet production rate during growth. The results of my study did not entirely support these conclusions because the daily fecal pellet production rate increased with the increase of body size of experimental animals.

It remains unclear why small animals have a higher specific egestion rate. Forbes and Lopez (1987) suggested that growth of small animals may be limited by their ability to pack sediment into their gut and to effectively absorb food. Since the time needed for digestion and absorption of food may impose additional constraints on the net energy intake of small worms, given their potentially shorter gut passage times, small worms should be able to process relatively greater amounts of sediment and retain it for a shorter period within the gut.

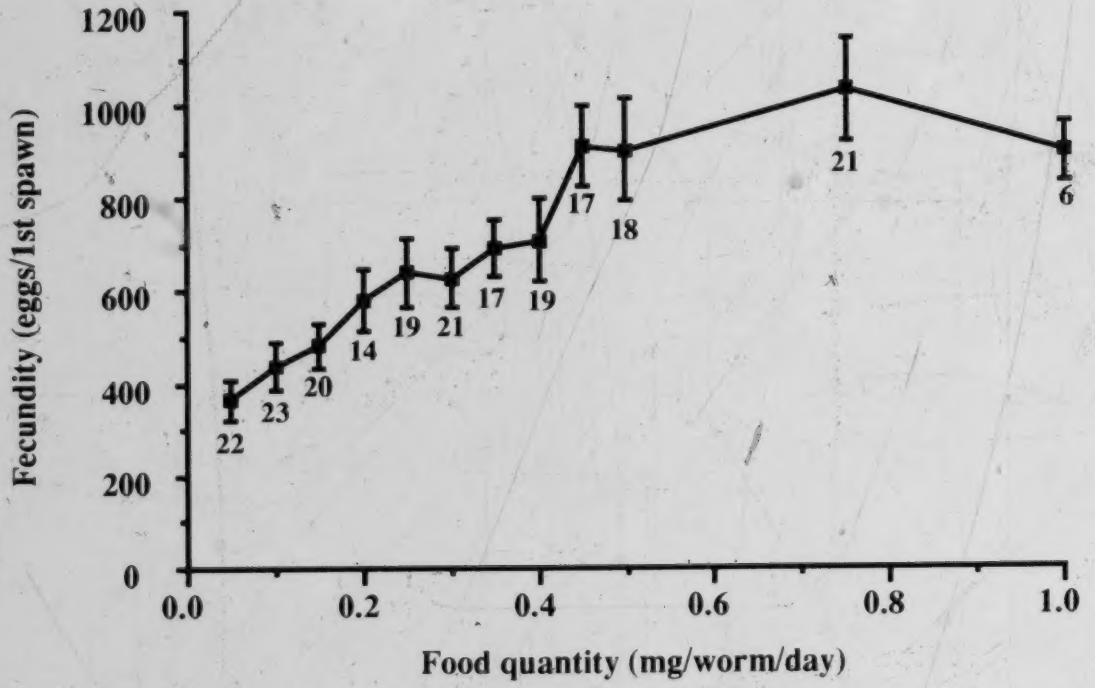

Figure IV-16: Effect of food quantity on fecundity of *Capitella* sp. (from lecithotrophic development). Data plotted are mean ± standard deviation with the sample size below each bar.

2. Egestion rate and food ration

The ingestion rate of deposit feeders are not only affected by body size of the animals, and temperature (Fobres and Lopez 1987), but also by the availability of food (quantity and quality of food) (Cammen 1980, Taghon and Greene 1990). There are several models on the functional responses of deposit-feeders to the organic content of sediment (Cammen 1980, Taghon 1981, 1988, Phillips 1984, Taghon and Greene 1990). Cammen (1980) found that the ingestion rate of 19 invertebrate species inversely varied with the organic content of the sediment. In my study, egestion rate (in terms of number or weight of fecal pellets per day) of *Capitella* of each size class decreased with increasing food rations. This supports Calow's Model (1983) that predicts an inverse relationship between the sediment-processing rate and food concentration. However, my results reject one of Cammen's hypothesis (1980) which predicts that deposit feeders have the ability to compensate for reduced food quality by increasing ingestion rate.

Based on the energy-maximization premise, Phillips (1984) predicted that a deposit feeder reaches its maximum sediment-processing rate at some intermediate food concentration. This model has been supported by at least two previous studies. Cammen (1989) found that the deposit-feeding amphipod *Corophium* feeds at the highest rate on sediment with an intermediate concentration of microalgae. Recently, Taghon and Greene (1990) reported that the sediment processing rate of the polychaete, *Arenicola pacifica*, reaches a maximum at an intermediate concentration of organic matter, decreasing at both lower and higher concentrations. My results also support this model as the egestion rate of *Capitella* sp. decreased with increasing food rations.

Cammen (1980) and Fobres and Lopez (1987) suggested above certain critical ingestion rate of sediment, the energy costs increase faster than the energy gained, and at this critical ingestion rate, the net rate of energy gain to the organism is maximized. Fobres and Lopez (1987) suggested that *Capitella* sp. I was energetically limited during

growth by the allometry of gut or respiratory surface area. Thus, the processing of additional sediment above an amount that could be effectively digested and absorbed, or metabolized by the oxygen reaching the mitochondria, would be an added cost with no additional benefit. All these may explain why feeding rate of a deposit feeder decreases at high food concentrations. However, it does not explain why growth rate (rates of absorption and digestion) of *Abarenicola pacifica* continues to increase as the organic content of the sediment increases when sediment-processing rate has reached maximum. It is clear that the decrease in sediment-processing rate observed at high sediment organic concentrations may not be associated with saturation of the animal's food-handling or energy-uptake capacities. Fobres and Lopez (1987) suggested that low ambient oxygen levels may suppress growth or anabolism. Also, feeding rate of animals may be limited energetically more by oxygen than by food supply in nature because the ability of digesting and absorbing food is better than that of processing oxygen to efficiently metabolize food. In conclusion, there is no clear explanation why feeding rates decrease at higher food concentrations.

3. Food ration and individual growth

Food rations affect the ingestion rates of deposit-feeding polychaetes and consequently affects growth rate. It has been well demonstrated in both laboratory experiments and field surveys that growth and body size of marine invertebrates are positively correlated to nutritional condition. Crump (1971) found that the sea star, *Patiriella regularis*, fed on freshly killed crabs, showed a mean increase of 62.9% of the original wet weight over a period of time, whereas animals that consumed greater quantities of dead fish showed a smaller total weight increase, indicating that growth rate relies not only on the quantity but also the quality of food. Nutrient enrichment was positively related to the increase of body length, segment number, and length per segment in a polychaete worm, *Streblospio benedicti* (Levin 1986, Levin and Creed 1986). This phenomenon has also been demonstrated in another polychaete species, *Polydora ligni*,

by Zajac (1986), who found that the individual growth rate of *P. ligni* increases with increasing food ration until it reaches at a maximum and then stays constant. During a series of studies of the nutrition of the polychaete *Capitella capitata* and its response to varying levels of food supply, Tenore and his colleagues (Tenore 1975, 1977a, 1977b, Tenore and Hanson 1980, Tenore 1981, Tenore and Chesney 1985) reported that the growth rate of *Capitella* populations depends on the amount of nitrogen in the food or amount of bacteria in the sediments. Grémare *et al.* (1988) found that the individual growth rate of *Capitella* sp. I is correlated with food quality and quantity. Marsh *et al.* (1989) reported that the growth of juveniles of *Capitella* sp. I was correlated with the levels of the amino acids such as, histidine phenylalanine, threonine, and valine; correlations with histidine and phenylalanine levels being the most significant. This study provided information that growth rate of *Capitella* sp. was affected by the quantity of food. In addition, my results indicate that *Capitella* sp. is very sensitive to food changes in its environment. A small change in food ration can be reflected in individual growth over a long period of time.

4. Food ration and sexual maturity

The proportion of breeding females of *Capitella capitata* type I increases with increasing food ration, which has been referred to as a decrease in maturation time by Grémare *et al.* (1988). Similar modifications of maturation time relative to food availability have already been reported for the polychaete, *Polydora ligni* (Zajac 1986). In addition, Wible (1984) found that increasing food availability led to a significant increase in the percentage of *Polydora nuchalis* reproducing, without affecting fecundity. In my study, *Capitella* with planktotrophic development showed a similar response. A high proportion of the worms that were fed at high food rations reached sexual maturity within 2.5 months, whereas a small proportion of them became sexually matured when fed at low food rations; no animal matured in the starved group. However, *Capitella* with lecithotrophic development in experiment III did not follow the same trend, in which

almost all worms in all food ration groups reached sexual maturity at the same time, although the animals fed at low food rations had much smaller body size and lower fecundity (eggs/brood) than those at a high ration.

5. Food ration and fecundity

Many studies have indicated that food availability in natural environments affects the reproductive output of marine invertebrates. Here, reproductive output (fecundity) can be defined as the number of eggs produced by an animal. Reproductive output of a given species is positively correlated to the available energy in its environments. This has been demonstrated in different phyla of animals, including three populations of the bird, *Pandion haliaetus*. Reduced food delivery is related to the increase of nesting loss and the decrease of clutch sizes (Poole 1982). Crump (1989) found that toads living in temporary ponds with low food availability, produce an unusually small clutch of large yolk-rich eggs, whereas toads in more permanent bodies of water that offer more food produce large clutches of small eggs. In an arthropod, *Paratenodera angustipennis*, higher prey density gave rise to a higher fecundity (Matsura and Morooka 1983). Spotted spider mites, *Tetranychus urticae*, living under good environmental conditions, had higher fecundity than those living under poor environmental conditions (Wrensch and Young 1975). Nutrient stress during gametogenesis can result in the production of fewer and/or smaller ova with reduced energy content (Bayne and Widdows 1978, Bayne *et al.* 1978, Bricelj *et al.* 1987). If nutrient stress is great enough, gametes will be resorbed (Bayne *et al.* 1983). For the bay scallop, *Placopecten magellanicus*, the initiation of gametogenesis is strongly linked to food availability (Thompson 1979, MacDonald and Thompson 1985a, 1985b). Differences in the amount of gonadal material produced are also correlated to available food supply, not only between sites but between years at the same site (MacDonald and Thompson 1985a, 1985b, MacDonald *et al.* 1987, Barber *et al.* 1988). However, some animals may keep their egg production constant by using reserve nutrients in the female body. For instance, Kessler (1971) found that among four spider

species (*Pardosa* spp.), all tend to keep the dry weight of eggs at a constant level under conditions of food shortage; some species produced the same number of eggs under conditions of food shortages as under maximum food supply.

In her laboratory experiments, Levin (1986) found that the number of ova/ovary, the number of brood pouches, the number of larvae/brood pouch, and the number of larvae/brood of the polychaete *Streblospio benedicti* increased with increasing food rations. In a copepod *Calanus marshallae*, egg production is highly dependent upon food supply; when deprived of food, individuals cease to produce eggs within 24 hours (Peterson 1988). In an insect, *Paropsis atomaria*, individuals fed on *Eucalyptus blakelyi* foliage with low levels of nitrogen laid fewer eggs at a slower rate than those fed on foliage with high levels of nitrogen (Ohmart *et al.* 1985). Thompson (1982) reported that both gonad production and test diameter of the sea urchin, *Stronglocentrotus droebachiensis*, were functions of food ration. Mckillup and Butler (1979) found that, as food availability decreases, the marine snail, *Nassarius pauperatus*, produced more eggs and more egg capsules per female, but less egg per individual capsule. Bradley (1984) found that food quantity did not affect the number of young of the desert scorpion *Paruroctonus utahensis*. Thus, reproductive response to food availability seems to be species-specific.

The population dynamics of *Capitella capitata* have been studied in laboratory cultures to ascertain the role of food availability in controlling 'boom and bust' patterns (Chesney and Tenore 1985, Grémare *et al.* 1988, 1989a, 1989b). In these studies, rapid population increase has been associated with high reproductive output (fecundity) and short generation time. It has also been demonstrated that reproductive output (fecundity) of *Capitella capitata* type I can vary dramatically over relatively short periods of time (Grémare *et al.* 1988, 1989a, 1989b). Although *Capitella* used in my study had lower growth rates, larger body sizes, and a higher fecundity than *Capitella capitata* type I, they showed similar response to food availability: fecundity increased with increasing food

ration.

6. Food ration and egg size

Few studies have demonstrated the effects of environmental factors on egg/ova size of marine invertebrates. Thompson (1982) reported that there were no significant differences between the mean diameters of the eggs produced by parents of the sea urchin, *Strongylocentrotus droebachiensis*, maintained at various food rations. Prey density did not affect the egg size of the mantis, *P. angustipennis* (Matsura and Morooka 1983). In the polychaete, *Streblospio benedicti*, the ovum diameter produced by females, with either planktotrophic or lecithotrophic modes of development, were unaffected by food ration (Levin 1986, Levin and Creed 1986). It is noted that the egg size used in previous studies was based on the measurements of dissected ova, which may not represent the real size of matured eggs. In this study, I found that matured egg sizes were influenced by food rations; animals at lower food rations produced larger eggs than those at high food ration. This supports Chia's (1974) hypothesis that animals tend to produce fewer, but larger eggs when food becomes scarce.

7. Food ration and egg quality

Thompson (1982) found that urchins fed with low levels of food release eggs with a lower lipid content per unit weight than eggs spawned by urchins fed with high rations. The same phenomenon has been demonstrated in the mussel *Mytilus edulis* (Bayne *et al.* 1978). Hirshfield (1980) found no difference in the energy content of eggs released by several groups of fish that were exposed to varying degrees of food stress. Moreover, there is some evidence that in marine invertebrates the eggs produced by food stressed adults are not only fewer in number, but also contain lower energy than those released by non-stressed parents (Bayne *et al.* 1978). Existing information indicates that even small changes in egg size or egg quality can be very important for embryo or larval survival. Kraeuter *et al.* (1982) showed that large eggs of a hard clam, *Mercenaria* (L.) and a bay scallop, *Argopecten irradians* (Lamarck) survived better than small eggs.

Marsh (1984) found that in the organgethroat darter, *Etheostoma spectabile*, offspring from larger eggs tended to be larger at hatching than those from smaller eggs although there was no effect of egg size on time to hatching. In my study, eggs produced by *Capitella* that fed at low food rations were larger and had a higher energy content than those produced by high food ration . This indicates that in *Capitella*, individuals at poor food condition can produce better quality eggs and it is assumed that these eggs are capable of developing into larger larvae or juveniles, and therefore they may have higher survival rate and this can be considered as a trade-off for the smaller number of eggs produced by these animals.

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CHAPTER V

EFFECT OF FOOD QUALITY ON GROWTH, FECUNDITY, EGG SIZE, AND EGG ENERGY CONTENT: TWO POPULATIONS BOTH WITH PLANKTOTROPHIC DEVELOPMENT

A. INTRODUCTION

A central issue in the study of reproductive ecology of marine invertebrates is how a species maximizes its reproductive output under different environmental conditions (Caswell 1981, 1982). Although egg size, energy content per egg, and fecundity are known to vary with environmental conditions among populations or individuals of a population, there are few studies that have examined the effects of physical or biological factors on egg size and fecundity under controlled conditions (McKillup and Butler 1979, Thompson 1982, 1984).

Capitella capitata (Fabricius) (Polychaeta: Capitellidae) from the northeastern United States has been divided into a complex of over six sibling species (Grassle and Grassle 1976, 1977, 1978, Grassle 1980). Although these sibling species show differences in their life history characteristics, which has been assumed under genetic control (Grassle and Grassle 1976, 1977, 1978, Grassle 1980), the relative importance of genetics and environment is not known.

Two populations of *Capitella* sp. were found in Barkley Sound, British Columbia (48°49' N and 125°09' W, Fig.1). The individuals of one population inhabited the egg capsules of the squid *Loligo opalescens* subtidally and the other was found in an intertidal

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mudflat in Grappler Inlet and fed mainly on detritus of the substratum. The subtidal animals fed on squid egg capsules, which could be determined by their cream color and fabric fecal pellets. They had larger body sizes and produced smaller eggs (94 µm in mean diameter along long axis of egg) but compensated by producing more eggs. The eggs of subtidal animals developed into planktonic trochophores that spent about four weeks in the water column before settling. By comparison, the intertidal animals had smaller body size, and produced fewer, and therefore larger eggs (125 µm in mean diameter) than those from the population using squid egg capsules.

Morphological features of the subtidal animals were similar to those of *Capitella capitata ovicula* described by Hartman (1969), whereas morphological features of the intertidal animals were similar to that of the original description of *Capitella capitata* (Fabricius 1870). Although animals from these two different habitats showed a number of differences in morphology and reproductive characteristics, I believe that they are the same species and the differences are mainly environmentally-induced. However, I can not preclude the possibility that they may be sibling species with overlapping life history characteristics. Also, the reproductive characteristics and body size of both groups of my study differ from those of the six sibling species of *Capitella capitata* described by Grassle and Grassle (1976). Since *Capitella capitata* is now used to refer to many sibling species around the world and no longer a functional species, I refer my populations to *Capitella* sp.

In this study, I addressed the following questions : (1) How does food quality affect egg size, energy content/egg, and fecundity ? (2) Are differences in life history characteristics between the two populations controlled genetically or merely a response to variables of the environment ? and (3) What is the relationship between egg size and fecundity ?

B. MATERIALS AND METHODS

1. Morphological and reproductive characteristics

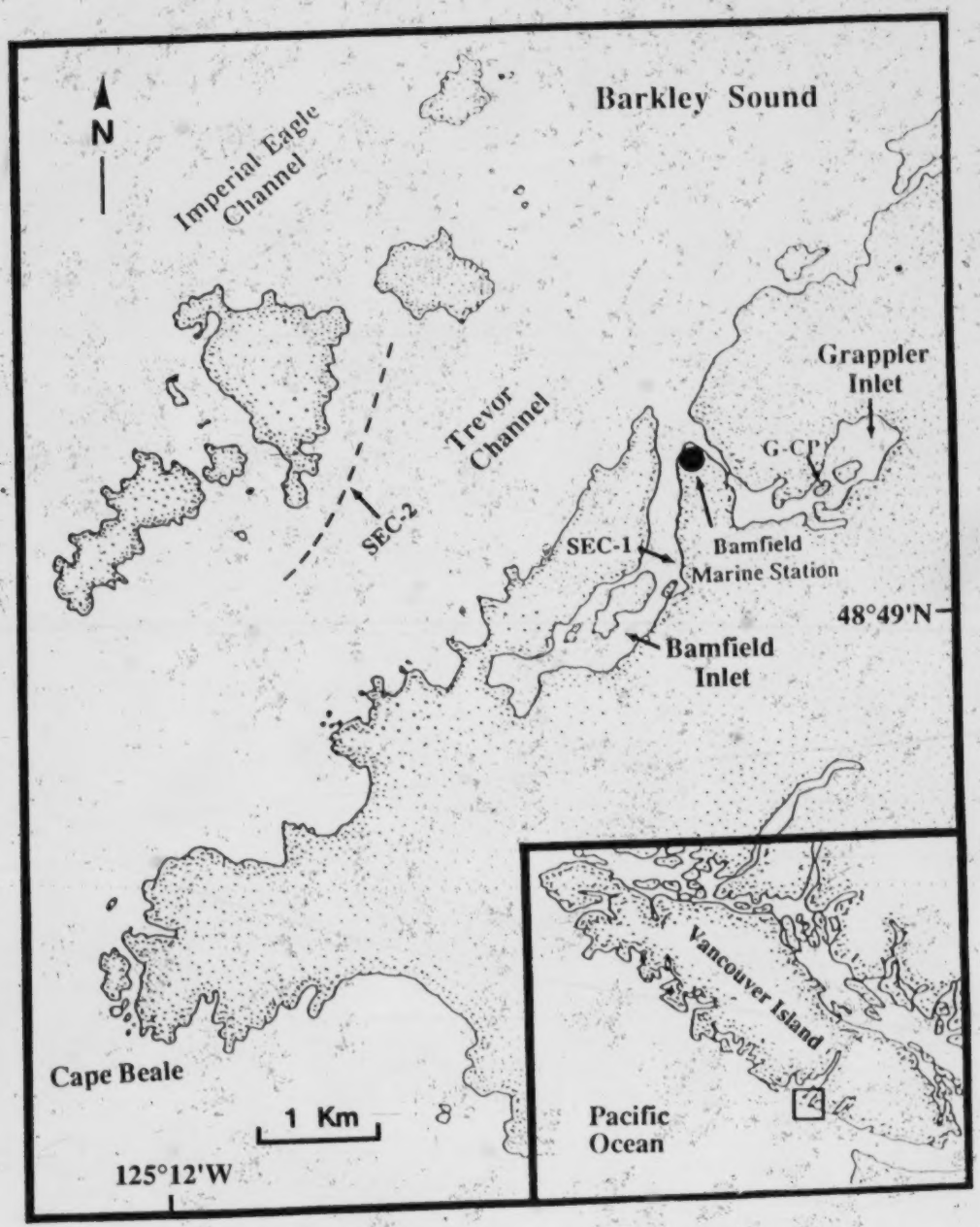
Pre-spawned and spawning animals were collected from both intertidal and subtidal habitats. Squid egg-capsules were collected subtidally using SCUBA, near the Government dock in Bamfield Inlet at a depth of 8-20 m in April, 1988 (Fig. V-1: SEC-1) and by dredging in Trevor Channel at a depth of 60 m from July through September, 1987 (Fig. V-1: SEC-2). Over 11% of 1400 squid egg capsules examined contained *Capitella* sp. Intertidal *Capitella* sp. were collected in July and August, 1987 from the mudflat of Grappler Inlet near the Bamfield Marine Station (Fig. V-1: G-CP). The distance between any two of the three collecting sites is about 1 mile.

In the laboratory, 20 pre-spawned females from each population were used for morphological studies (sex was determined by examining ovaries and copulatory spines). Each selected worm was relaxed in 0.36 M $MgCl_2$ and the body length was then measured under a dissecting microscope equipped with an ocular micrometer. The wet weight of each worm was determined by using a microbalance, and dry weight was determined after they had been dried in an oven at 100°C for 12 h.

The wet weight and dry weights of eggs and the somatic tissues from pre-spawned females were measured. The organic carbon content of the eggs and somatic tissues was measured using the methods of Parsons *et al.* (1984). Organic carbon weight (μg) was converted to joules (J), by the following equation: $\mathbf{1\ \mu g^{C} = 3.9 * 10^{-2}\ J}$ (Parsons *et al.* 1984).

To determine fecundity, egg size, egg energy content, and total energy per brood, pre-spawned females were selected randomly from each population and each animal was isolated in a culture beaker. These animals spawned in the laboratory within four days. After all the eggs had been released into the tube, the worm was gently removed from the tube. Tubes were then opened carefully with fine needles under a dissecting microscope and the eggs were counted. For animals from squid egg-capsules, it is not practical to

Figure V-1: Map of the sampling areas of subtidal and intertidal populations of *Capitella* sp with planktotrophic development. SEC-1 indicates the sampling site of squid egg capsules in Bamfield Inlet; SEC-2 indicates the sampling site of squid egg capsules in Trevor Channel; G-CP indicates the location of the intertidal population in Grappler Inlet; ----- indicates the dredging rout.


N
Barkley Sound
Imperial Eagle Channel
Trevor Channel
SEC-2
SEC-1
Grappler Inlet
G-CP
Bamfield Marine Station
48°49'N
Bamfield Inlet
Cape Beale
1 Km
125°12'W
Vancouver Island
Pacific Ocean

count all of the eggs released by a worm because of high fecundity. Therefore, each worm tube (with newly-released eggs) was divided into ten equal segments under a dissecting microscope with the aid of an ocular micrometer. Three segments were selected randomly and the eggs in these segments were counted and averaged; the mean was multiplied by ten to obtain the total number of eggs produced by that animal. This method is not as accurate as counting all of the eggs, but it should not affect my conclusion since the difference in fecundity between treatment groups is so large.

The long and short axes of twenty to thirty newly-released eggs from each spawned individual were measured with a Zeiss compound microscope equipped with an ocular micrometer. The egg volume (V) was calculated using the following formula: $V=(4/3)\pi A^2 B$, where **A** and **B** are the length of short and long axes of the egg, respectively.

Energetic content of the eggs was measured using the procedure described by Parsons *et al.* (1984) and McEdward (1986) (also see the details in Chapter III). Three replicates from the same female were used, each containing either 150 or 500 eggs, depending on the size of the eggs. The total energy of the released eggs was obtained by multiplying the number of eggs by the energetic content per egg.

Larval pelagic period was also determined following the methods outlined in Chapter III.

2. Laboratory experiments

One parent from each population was used in this experiment. Two hundred sibling juveniles from a single female from either the intertidal or subtidal population were placed into four plastic trays (50 individuals per tray). Each plastic tray measured $10*10*10\ cm^3$. Animals in two trays were supplied with squid egg capsules as food and the substratum while animals in the other trays were supplied with ground *Ulva* for food at ration of 2 mg dry weight/worm/day and fine sand (<0.5 mm grain size) for the substratum (Fig. V-2). All trays were partially-submerged in flowing filtered (50 μm)

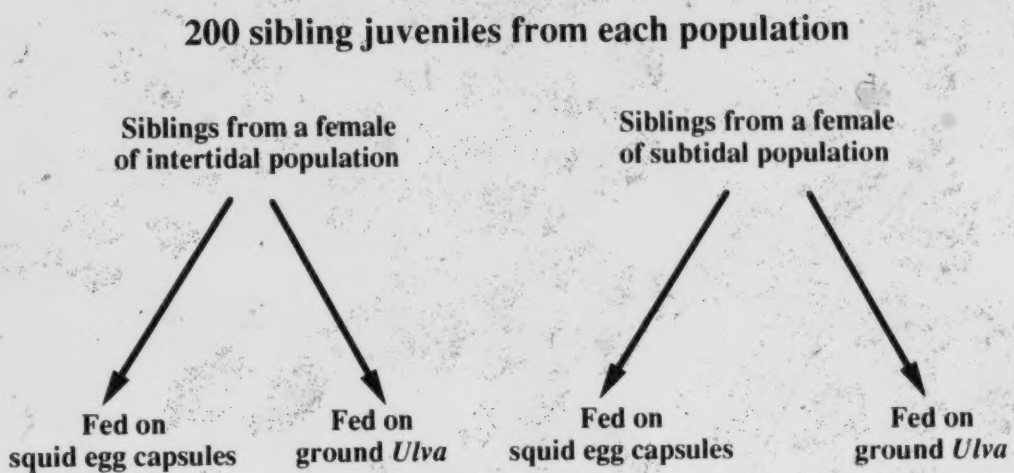

200 sibling juveniles from each population
Siblings from a female of intertidal population
Siblings from a female of subtidal population
Fed on squid egg capsules
Fed on ground *Ulva*
Fed on squid egg capsules
Fed on ground *Ulva*

Figure V-2: Outline of experimental design for experiments assessing the effects of diet quality on growth and reproduction of planktotrophic developing *Capitella* sp. from subtidal squid egg mass and from intertidal mudflat.

seawater at ambient sea water temperature (10 - 11°C). Ground *Ulva* used in this experiment contained 30% carbon, 3.5% nitrogen, and 4.4% of hydrogen in dry weight; contained 11.7 joules/mg dry weight. To my best knowledge, the chemical composition of squid egg capsules is not available. However, previous study has indicated that ovary and reproductive organs (oviduct and oviductal gland) of *Loligo opalescens* contained up to 68% protein and 7% lipid of the dry weight (Giese 1969). Thus, I assumed that the egg capsules of *Loligo opalescens* were much more nutritious than ground *Ulva*.

Body length, body width at the fifth setiger, and number of setigers were determined by examining a random subset of ten individuals from each tray biweekly until they began to reproduce. The selected worms were first transferred to a culture dish with a small amount of sea water; and then relaxed in 0. 36 M $MgCl_2$ solution after the worms had crawled out of their tubes. Measurements were made under a dissecting microscope equipped with an ocular micrometer. The animal was immediately returned to the original tray after measurement.

Body volume (V) of each individual was calculated according to the following equation: $V=\pi(D/2)^2L$, where **D** and **L** are the diameter (width) and length of each worm.

Growth rate of experimental animals was calculated using the equation:

$$G=(V_t-V_{t-1})/T_t-T_{t-1}$$

and average body volune-specific growth rate, was calculated by following the equation:

$$G'=\{(V_t-V_{t-1})/[(V_t+V_{t-1})/2] * (T_t-T_{t-1})\}*100\%$$

where V_t and V_{t-1} are the average body volume at experimental time **t** and **t-1**, respectively; T_t and T_{t-1} are the number of days that experiments have been conducted at interval **t** and **t-1**, respectively.

The dry weight of the worms was obtained by placing each worm in an oven at 110°C for 24 h: and its dry weight was measured to 0.01 mg. I found a positive

relationship between body volume (Y, mm^3) and body dry weight (X, mg), which can be expressed in the following equation: **Y=44.4 X - 26.1** (n=48, r^2=0.92, F=62.6, P<0.001).

Fecundity, egg size, egg energy content, and total energy per brood of the laboratory reared animals were determined in the manner described in section **I**.

3. Data analyses

Statistical tests were carried out with SPSS software (1985). All analyses were performed on untransformed data. Analyses of covariance of regression lines between body size and experimental times under different diet condition were calculated. The unpaired t-test was used to assess differences in reproductive parameters of the animals from the two field populations, and of the laboratory reared animals. One-way ANOVAs and Student-Newman-Keuls multiple comparison tests were used to test for differences in fecundity, egg size, and energetic content among the groups from both field and laboratory experimental reared populations (Zar 1984).

C. RESULTS

Table V-I summaries the main morphological and life history features of the two field populations as well as the results of unpaired t-test for each parameter. Results indicate that animals from subtidal population had longer bodies (121 mm) compared to the intertidal group (74.13 mm) (Table V-1). These longer animals had approximately 20% more setigers and were twice as heavy as animals from intertidal population.

Although animals from subtidal population contained about 2.6 times more energy than the animals from intertidal population, 75% of this energy was in reproductive tissue and only 25% of total energy in body tissue (Table V-1). By comparison, intertidal animals only devoted 45.9% of total energy to reproductive tissue (Table V-1). Energy in somatic tissue was not significantly different between subtidal and intertidal animals (Table V-1). It should be pointed out here, however, since these data

Table V-I: Morphological features and reproductive characteristics of two field populations of *Capitella* sp. with planktotrophic development. The results of two-tailed unpaired t-tests are also shown. Values are mean ± standard deviation (sample size).

	Animals of subtidal population	Animals of intertidal population	T-test T-value	P
Body features				
Body length(mm)	121.00±25.40 (20)	74.13±9.34 (16)	-7.17	<0.001
Body Wet Weight (mg)	191.40±63.89 (20)	38.86±7.62 (16)	9.46	<0.001
Body Dry Weight (mg)	27.11±13.15 (20)	13.38±1.19 (16)	3.96	<0.001
Total energy (J)	223.55±71.14 (20)	115.33±4.1 (16)	7.74	<0.001
Energy in eggs (J)	168.18±61.42 (20)	69.01±4.25 (16)	8.37	<0.001
Energy in somatic tissue (J)	55.37±20.11 (20)	46.32±1.39 (16)	1.8	>0.05
Reproductive characteristics (based on different specimens from those above)				
Egg diameter(µm)	94.10±15.69 (260)	122.90±16.16 (860)	-41.8	<0.001
Egg Vol($mm^3 x10^{-3}$)	0.44±0.08 (260)	0.97±0.27 (860)	-3.46	<0.001
Energy/egg (10^{-3}J/egg)	4.88±0.66 (39(500))	18.76±3.94 (86(500))	-20.67	<0.001
Fecundity (# of eggs)	34352±22325 (28)	4991±4174 (43)	6.93	<0.001
Total energy/spawn(J)	167.47±108.84 (28)	93.63±78.30 (43)	1.12	>0.05
Pelagic period of larvae	> 3 weeks	2-3 weeks		
Juvenile length(µm) (newly-metamorphosed)	275 - 350	310 - 490		

were based on pre-spawning individuals, the degree of maturity of individuals from each population may not be absolutely identical, which may have yielded a bias in estimating reproductive efforts.

Subtidal individuals produced smaller eggs than intertidal animals: the egg diameter of subtidal animals was about 30 μm smaller than that of intertidal animals while the egg volume of subtidal animals was less than 50% of that of interdal animals (Table V-1). Eggs from intertidal individuals contained about 4 times higher energy content than those from subtidal individuals. However, subtidal individuals produced almost 7 times more eggs than intertidal individuals (Table V-1). On average, subtidal animals invested approximately twice as much energy in eggs as those from intertidal population, but this difference was not statistically significant because of large variations within each population (Table V-1).

Eggs from subtidal individuals developed into small trochophores that hatched out from the adult tube within a week. These trochophores were planktotrophic and pelagic for more than 3 weeks before becoming competent to settle. Mortality of these trochophores was very high (more than 95%) under laboratory culture conditions. Newly-metamorphosed juveniles measured 275 to 350 μm in body length. By comparison, eggs from intertidal individual developed into larger trochophores that hatched also within a week. The pelagic period of these trochophores was shorter than 3 weeks. Mortality of these trochophores was also lower than those from subtidal population. Juveniles of intertidal populations measured about 310 to 490 μm in body length.

1. Effect of food quality on growth

Under identical laboratory conditions, the body volumes of animals from the intertidal population that fed on squid egg-capsules increased much faster than that of their siblings fed on ground *Ulva* (Fig. V-3A, Ancova test: $F=9.8$, $P<0.05$; $F=7.8$, $P<0.05$ for slope and elevation, respectively). Animals from the squid egg capsule,

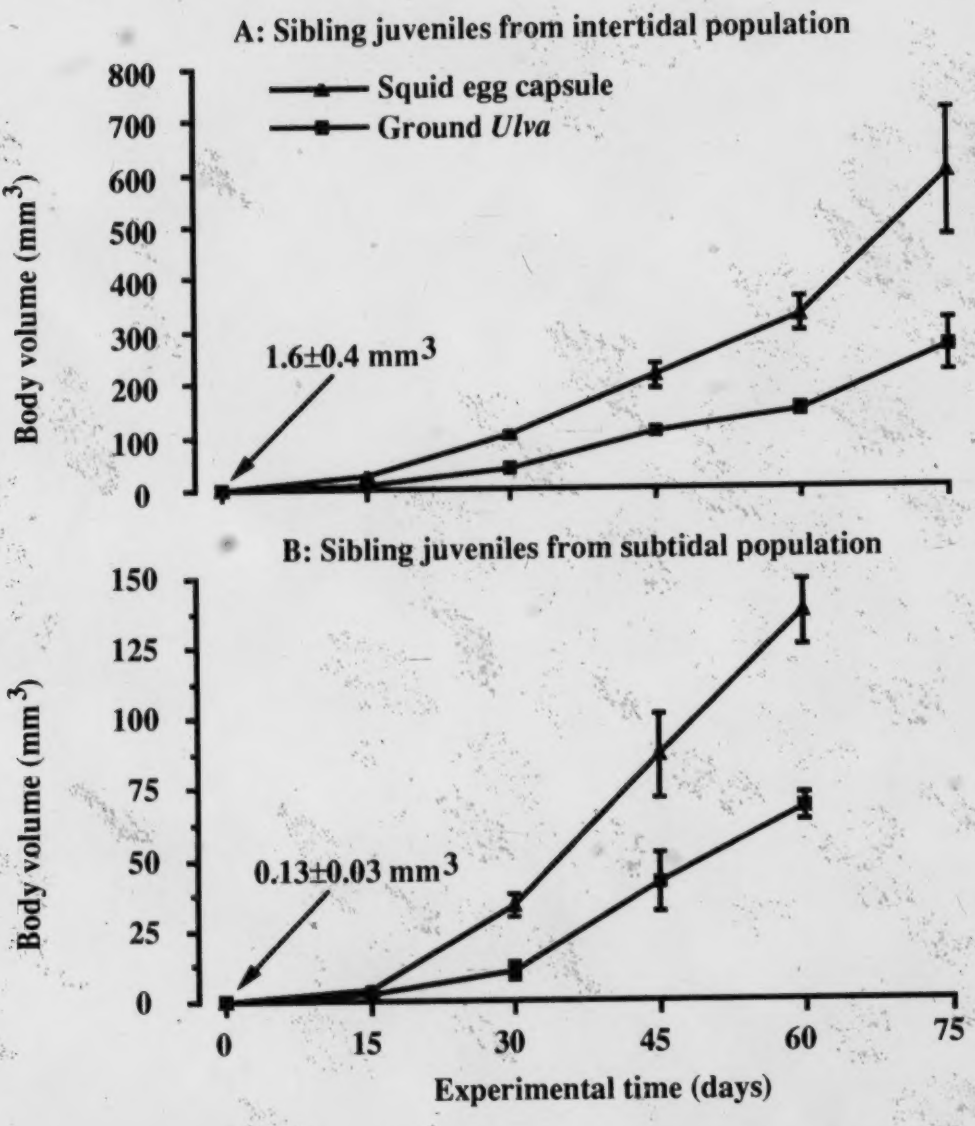


Figure V-3: Effect of food quality on body volume changes of *Capitella* sp. with planktotrophic development. Values plotted are mean ± standard deviation from measurement of 20 animals. Note: A and B are plotted on different scales as the initial size of juveniles in B are much smaller than those in A; Juveniles in B are 3 weeks younger than those in A at the beginning of experiments.

when fed with different diets, also showed different increases in body volume (Fig. V-3B, Ancova test: $F=10.1$, $P<0.05$; $F=5.1$, $P>0.05$ for slope and elevation,respectively). When fed on squid egg-capsules, animals from both populations grew twice as large as their siblings that fed on ground *Ulva* over 60-80 days.

As expected, the number of setigers of animals increased very rapidly at young stages, thus, effects of diets on the number of setigers were more noticeable within a period of rapid increasing in the number of setigers (Fig. V-4). Animals from both populations that fed upon squid egg capsules added more setigers than those fed upon ground *Ulva* within the same time period.

Figure V-5 gives more visual indication on how the diet affects animals' growth rate. In general, animals fed on squid egg capsule had higher growth rate in term of net daily increase in body volume than those fed on ground *Ulva* .

Figure V-6 provides specific growth rate of animal. It indicates that young animals had higher specific growth rate than olders. In Figure V-6A, animals that fed on squid egg capsule had specific growth rate over 11% within the first 15 days, whereas animals that fed on ground *Ulva* only had about 8% . In Figure V-6B, animals that fed on squid egg capsule had specific growth rates over 12% within the first 15 days whereas those fed on ground *Ulva* about 11%. It should be noted that animals fed on squid egg capsule or even on ground *Ulva* in Figure V-6B had higher body-specific volume growth rates than those fed on squid egg capsule in Figure V-6A within the first 15 days, which further indicated that young animals had higher specific growth rate than older animals since animals in B were about 3 weeks younger, therefore much smaller than those in A at the beginning of the experiments.

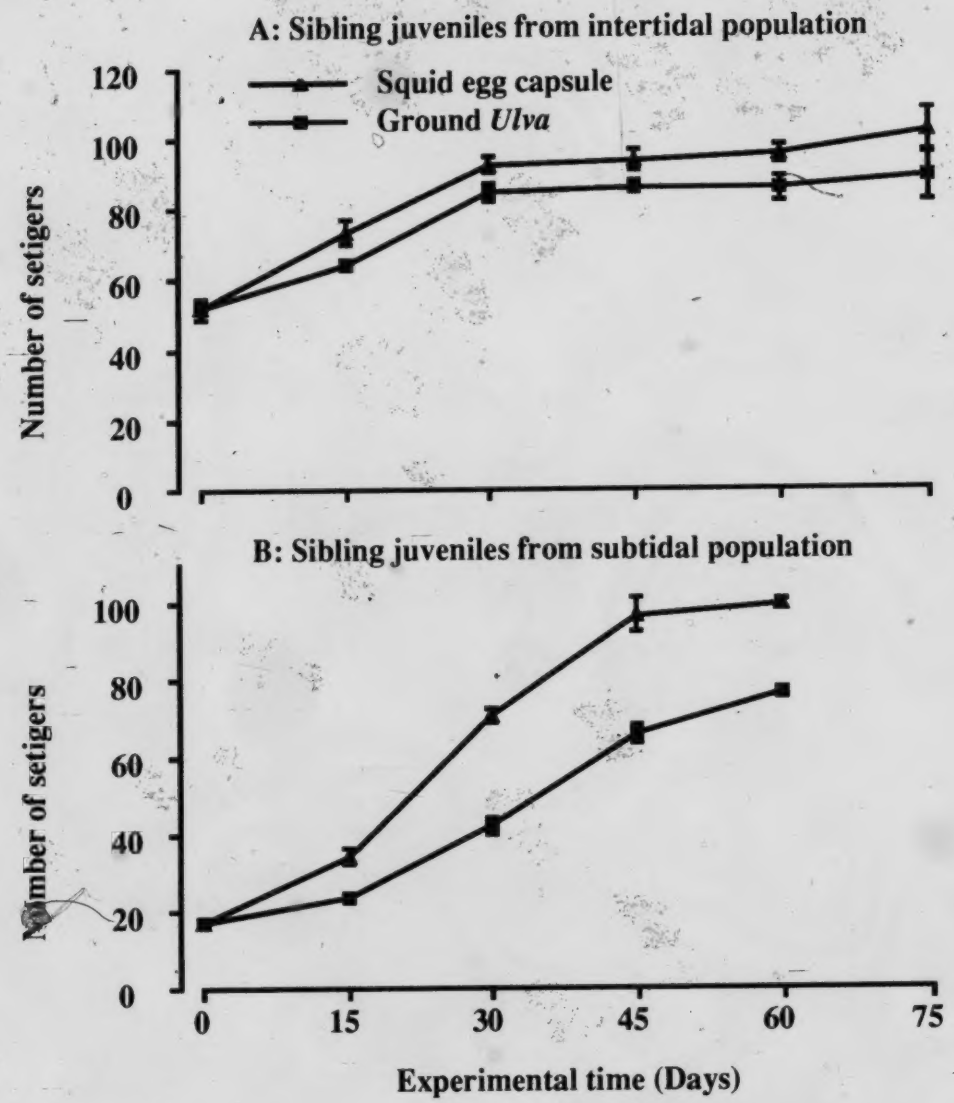


Figure V-4: Effect of food quality on changes in the number of setigers of *Capitella* sp. with planktotrophic development. Values plotted are mean ± standard deviation from measurement of 20 animals. Juveniles in B are smaller and younger than those in A at the beginning of experiments.

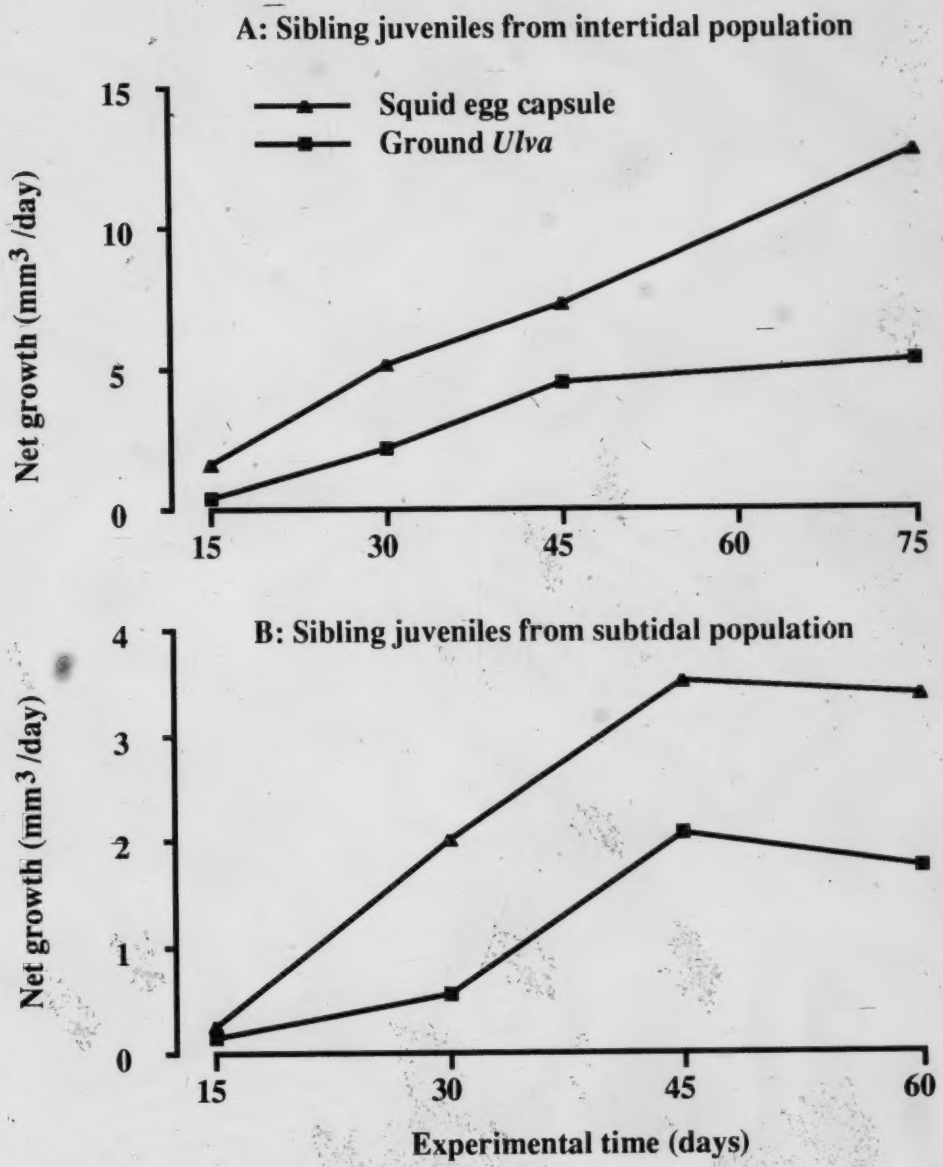


Figure V-5: Effect of food quality on growth rate of *Capitella* sp. with planktotrophic development. Growth rate is recorded as the increase in body volume per day.

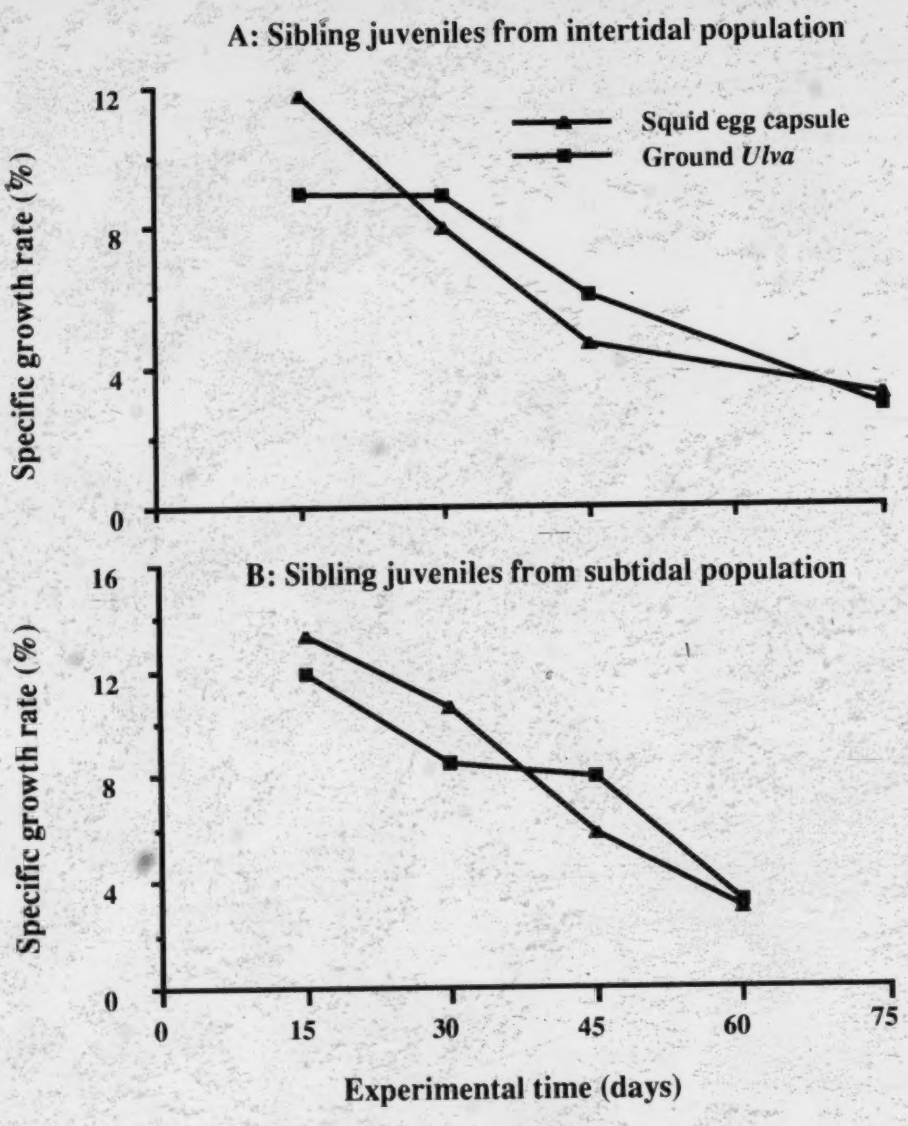


Figure V-6: Effect of food quality on specific growth rate of *Capitella* sp. with planktotrophic development. Specific growth rate is recorded as the proportional increase in body volume per day (daily increase in body volume divided by mean value for body volumes at the beginning and the end of each intertidal)

Figures V-3 and V-4 were plotted on different scales because the juveniles from the subtidal population were much younger (post-settling) and smaller than juveniles from the intertidal population. Because the growth rate of *Capitella* sp. changed with initial body size, it was impossible to compare the growth rate for these two experimental populations.

2. Effect of food quality on fecundity, egg size and energy content

Results summarized in Table V-II indicate that siblings of the intertidal population produced 5 times more eggs when fed with squid egg-capsules than when fed with ground *Ulva* (unpaired T-test: $T=6.91$, $P<0.001$). Their eggs, however, were much smaller (unpaired T-test: $T=-9.45$, $P<0.001$) and contained lower egg energy content (unpaired T-test: $T=12.81$, $P<0.001$). The total egg volume per brood of individuals fed squid egg capsules was twice as large as that of individuals fed on ground *Ulva* (unpaired T-test: $T=4.89$, $P<0.001$). Animals fed on squid egg capsules invested twice as much energy in their first spawn as their siblings fed on ground *Ulva* (unpaired T-test: $T=3.32$, $P<0.01$).

Siblings from the subtidal population (in squid egg capsules) followed the same trend. Results of Table V-II indicate that *Capitella* sp. siblings when fed on squid egg-capsules were five times more fecund than those fed on ground *Ulva* (unpaired T-test: $T=3.36$, $P<0.001$), produced much smaller eggs (unpaired T-test: $T=-9.23$, $P<0.001$), and contained less energy per egg (unpaired T-test: $T=-27.43$, $P<0.001$).

When the data from the field populations were compared with those from the laboratory reared animals, it was found that fecundity, egg size, and egg energy content were the same when fed on the same kind of diet (Table V-III). Animals fed on ground *Ulva* had lower fecundity and produced larger, higher-energy eggs than animals fed on squid egg capsules. However, the total energy invested in the eggs were not significantly different among the six groups (Table V-III).

Table V-II: Effects of food quality on fecundity, egg size, egg energy content, and total reproductive output of two *Capitella* sp. populations with planktotrophic development. Values are mean ± one standard deviation (sample size).

	Siblings from a subtidal female fed		Siblings from an intertidal female fed	
	Squid egg-capsules	Ground *Ulva*	Squid egg-capsules	Ground *Ulva*
Eggs/breed worm (fecundity)	25515±9055 (21)	7947±3037 (18)	27793±22146 (33)	4725±2653 (46)
Egg diameter (µm)				
Short axis (A)	92.2±7.8 (180)	113.3±20.3 (180)	101.5±11.4 (540)	122.8±7.8 (660)
Long axis (B)	97.4±7.3 (180)	124.9±24.0 (180)	113.7±13.6 (540)	135.9±9.0 (660)
Egg Volume (mm^3*10^{-3})	0.44±0.10 (180)	0.91±0.46 (180)	0.64±0.22 (540)	1.08±0.19 (660)
Energy content ($J*10^{-3}$/egg)	4.25±0.78, 18(3)	11.23±6.36, 12(3)	5.69±2.57 (27(3))	12.48±1.44 (33(3))
Total egg volume/spawn (mm^3*10^{-3})	11201±3972, 180	7272±2779 (180)	13430±8288 (540)	5478±2836 (660)
Total energy/spawn (J /egg)	108.5±38.5 (18)	89.2±34.1 (12)	117.2±82.9 (27)	63.45±35.1 (33)
Larval pelagic period	>3 weeks	2.5 weeks	>3 weeks	2.5 weeks

About 10% of the individuals from both laboratory populations did not change their reproductive characteristics with the change of diet. Fecundity, egg size, and egg organic carbon of these 10% worms showed no significant differences from those of their parents even though the types of food had been reversed.

Another important but expected feature was that the small eggs invariably developed into smaller trochophores and had a longer pelagic life than those developed from larger eggs (Table V-II).

D. DISCUSSION

In this study, great variation in fecundity, egg size and adult size have been recorded from each field population. Although part of these variations could be the result of relatively small sample sizes in my study, a major proportion of these variations should be the result of genetic or physiological differences in the animals. These differences provide the population flexibility in reproduction and growth both in the field and laboratory. Laboratory results from my study further indicated that even sibling offspring of a single female can have different response to identical environment conditions. As I have indicated in the results, when sibling offspring of a single female from either the subtidal population or intertidal population were fed with different diets, most animals responded to the type of diet that they were provived, by changing their growth rate, fecundity, egg size, and egg energy content, which appears to indicate that reproductive characteristics of these animals were environmentally-determined; whereas about 10% of their siblings had similar fecundity, egg size, and egg energy content to their mother, which seems to indicate that reproductive characteristics of those animals were genetically-programmed.

Table V-III: Results of ANOVAs and Student-Newman-Keuls multiple comparisons tests of differences in fecundity, egg size, egg energy content, and total reproductive output among planktotrophic developers of *Capitella* sp. from different populations and fed on different diets. Values that did not differ at the 0.05 level are joined by a solid line.

	One-way ANOVA		SNK-test
	F	P	5%
Fecundity	27.3	<0.0001	A B C D E F
Egg volume	46.1	<0.0001	A B C D E F
Energy content	266.2	<0.0001	A C B D E F
Total egg volume/spawn	48.7	<0.0001	A B C D E F
Total energy/spawn	1.97	>0.05	A B C D E F

Captions for Table III:

A-- *Capitella* sp. from field intertidal population.

B-- Laboratory reared *Capitella* sp. from a single female of the intertidal population and fed on ground *Ulva*.

C-- Laboratory reared *Capitella* sp. from a single female of the subtidal population and fed on ground *Ulva*.

D--Siblings of B fed on squid egg capsules.

E--Siblings of C fed on squid egg capsules.

F--*Capitella* sp. from field subtidal population.

There appears to be a conflict about sibling offspring of a single individual having two different controlling system on their reproductive characteristics and growth. But there are two possible alternative explanations: (1) If the sibling offspring are genetically identical, they must have both genetically-controlled and environmentally-determined programs occurring simultaneously, or (2) the sibling offspring of *Capitella* are not genetically identical, genetic information not being evenly distributed among the gametes during the gametogenesis. Each of these will give the population of *Capitella* high flexibility so that *Capitella* can be very successful in a variety of environmental conditions. Unfortunately, I do not have any direct evidence to prove or disprove any of these hypotheses at this moment.

One of the important conclusions I can draw in this study is that ecological barriers between *Capitella capitata* and *Capitella capitata ovicula* collected from Barkley Sound in British Columbia were obscure and weak. These two populations have not been entirely separated by ecological barriers and speciation may have not occurred in this situation. However, ecological separation has acted on these two populations as I see numbers of differences in adult size, morphology, reproductive characteristics of two populations. Under laboratory conditions, sibling offspring of subtidal females seemed to have different growth rates although this might be the bias of my laboratory culture conditions.

Although fecundity has been used as an indicator of reproductive effort and life history of marine invertebrates (Vance 1973a, 1973b, Christiansen and Fenchel 1979, Grahame and Branch 1985), it is not, as my data demonstrated, a conservative reproductive parameter; it can vary with adult nutritional state or body size. For instance, Fletcher (1984) showed that the amount of environmentally-determined variation in reproductive output exceeds interspecific differences previously described in four species of limpets. Among environmental factors, both the quality and quantity of food have been considered to be the most important factor responsible for variation in fecundity of marine invertebrates. Zajac (1986) found that food supply is positively correlated with fecundity

of *Polydora ligni*. Levin and Creed (1986) also indicated that higher food levels led to an increase in the number of ova per ovary and in the number of larvae per brood pouch for *Streblospio benedicti*. In contrast, the number of eggs and egg capsules produced by starved *Nassarius pauperatus* is positively correlated with the degree of starvation of individual animals in a population, although the average number of eggs per capsule is negatively correlated with the degree of starvation (Mckellup and Bulter 1979). It appears that there was a potential trade-off between fecundity and survivorship in *Nassarius pauperatus*; animals with higher reproductive effort had lower survivorship (McKillup and Bulter 1979). Tenore (1975, 1977, 1981) found that population growth of *Capitella capitata* was positively correlated with food supply. Grémare *et al.* (1988, 1989a, 1989b) found that the number of fertile segments, the number of eggs per fertile segment, and the reproductive output were affected by food quality in *C. capitata* Type I. Because the gametes inside the body were used as the indicator of fecundity in the previous studies, this may have led to inaccurate conclusions because not all the gametes in the studied organisms were released and fertilized. My study is the first to conduct these experiments under controlled conditions and to calculate fecundity based on fertilized eggs. Also, my study is the first to indicate that large variations (5-7 times) in fecundity of a single species is the result of food quality.

Because egg size for a given species is believed to be relatively constant and the egg quality is correlated to egg size, egg size is probably the most frequently reported life history character for marine invertebrates. There is, however, evidence indicating that egg size can vary with environmental changes in copepods (Brambilla 1982), echinoderms (Thompson, 1982, Turner and Lawrence 1979), fish (Bagenal 1969, 1971, Lee 1983), salamanders (Kaplan 1980a, 1980b, Kaplan and Cooper 1984), and frogs (Crump 1981, 1984). Recent studies revealed that egg sizes of many echinoderms vary with adult body size, successive spawning, and adult nutritional condition. For example, Turner and Lawrence (1979) found that variations in egg volume that was significantly different

among specimens within the same species, or between years for 11 species of echinoderms. McEdward and Carson (1987) also found that mean egg volumes of the starfish *Solaster stimpsoni* were significantly different among females at each of four locations. All of the above mentioned studies on variability in egg size are based on animals collected from natural populations, which may have been subjected to changes in a number of environmental factors. Experimental studies described in my paper provided the first set of data collected under controlled conditions where the only variable was food quality. My study shows that animals reared under one kind of food produce a greater number of smaller eggs than those reared on another kind of food.

Although the energetic content (joules/egg) generally increased with egg volume, no clear relationship was evident. For example, in the green sea urchin *Strongylocentrotus droebachiensis*, the lipid content and energy content of the eggs were significantly lower in a low food ration group, but the mean egg diameter did not differ from that produced by parents maintained at a higher food ration (Thompson 1984). The same phenomenon has been demonstrated in the mussel *Mytilus edulis* in which the eggs produced by stressed adults are not only fewer in number but also poorer in quality than those produced by non-stressed individuals (Barnes *et al.* 1975). The organic content of eggs of *Solaster stimpsoni* varies among animals from different locations and among females within the same population (McEdward and Carson 1987). McEdward and Coulter (1987) also found that egg volume and energetic content were not positively correlated in siblings of the sea star *Pteraster tesselatus*. My experiments reveal that polychaetes that fed on squid egg-capsules produced a greater number of smaller, poorer quality eggs (in term of energy content per egg) than animals fed on ground seaweed. I conclude that the relationship between egg size and parental investment per eggs is determined by the environmental conditions (that affects embryonic or juvenile survival), and that the pattern of correlation between egg size and egg energy content among populations can not be generalized.

A number of previous studies indicated that larger eggs usually result in larger offspring at hatching (Bagenal 1969, Gall 1974, Capinera and Barbosa 1976, Barbosa and Capinera 1978, Crump 1984, Marsh 1986, Rhymer 1988, Williamson and Bull 1989) and/or result in offspring that have better survival rate or faster growth rate (Bagenal 1969, Gall 1974, Kraeuter *et al.* 1982, Williamson and Bull 1989). In this study, I found that the larger eggs produced by individuals fed on *Ulva* developed into larger trochophore larvae. These larvae have a shorter pelagic period than those developed from smaller eggs. The size of juveniles developed from larger eggs are also larger. All these indicate that even small changes in egg size may be important in offspring survival. However, it is also common that larger eggs develop more slowly than small ones in other groups of invertebrates (see Spight 1975). Crump (1981) postulated that under some conditions, larger eggs are expected to do better than smaller eggs, but under other conditions smaller eggs would have greater fitness; thus variability in egg size should be adaptive given the uncertainty and fluctuation in the environment. Berven and Chadra (1988) also suggested that optimal egg size is correlated with environmental factors; they found that in the wood frog (*Rana sylvatica*), larvae from small eggs had a longer larval periods and a larger size at metamorphosis than larvae derived from large eggs at low densities and high food levels, whereas larvae from small eggs had longer developmental periods but were smaller at metamorphosis than larvae from large eggs at high densities.

Presently, there is no clear explanation as to why animals fed on high quality food produced more, but smaller eggs, and had longer lived larvae than those fed on poor quality food. Smith and Fretwell (1974) have suggested that females are selected to increase egg size in order to produce larger and competitively superior juveniles at a time when food is in low supply and when juvenile density is high or when there is high predation pressure on the juveniles. Chia (1974) suggested that marine invertebrates tend to produce fewer and larger eggs when food is limited, and produce more and smaller eggs when food is abundant; the trade-off between the two modes of reproduction appears

to be between the higher survivorship (fewer but larger eggs) and the greater dispersion (more but smaller eggs). My results appear to be consistent with these predictions. In this study, I found that individuals from different environments invested similar amounts of energy in their eggs (Table III), but showed differences in life-histroy traits. These further indicate that this species has high flexibility in its life-history strategy, which are highly adaptive to environmental changes. Hughes and Roberts (1980) found that the marine snail, *Littorina rudis*, under high predation pressure from crabs at one site produced larger eggs, and hence larger juveniles and that snails at another site with no predation had greater fecundity and smaller eggs. Larger eggs are also associated with conditions of higher desiccation.

After analyzing 64 species of molluscs and polychaetes, which have been reported to be poecilogonous, Hoagland and Robertson (1988) concluded that the pattern of development is a generally reliable species character in invertebrates, and differences often signify unrecognized species. My study has clearly demonstrated a high flexibility in fecundity and egg size existing in a single species of *Capitella* sp. Gibson and Chia (1989) also found that *Haminoea callidegenita* can produce two types of offspring; embryos in the same egg mass can hatch as either veligers or juveniles (intracapsule metamorphosis), and the intracapsule metamorphosis is induced by a factor in the egg mass jelly. In conclusion, this study is the first demonstration from the controlled experiments that highly flexibile reproductive characteristics exist within a species.

It is known that many populations of *Capitella* along the Pacific coast of North America live in squid (*Loliqo* spp.) egg capsules (Hartman 1969). In this study, I found that over 10% squid egg capsules collected from my study sites contained *Capitella* and the number of worms in egg capsules varied from 1 to 4 per squid egg capsule. This study indicates that *Capitella* fed on squid egg capsules attained a larger body size and produced more offspring than their sibling fed on ground *Ulva*. A preliminary observation indicates that the presence of worms in squid egg capsules can increase

mortality of squid embryos. However, laboratory observations also indicate that newly-hatched juveniles of squid can feed on newly-hatched *Capitella* trochophores, which indicates that squid may also benefit from the presence of worms. Future studies of the association between *Capitella* and *Loligo* should be interesting.

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CHAPTER VI

EFFECT OF DIET TYPE ON GROWTH, FECUNDITY, EGG SIZE, AND EGG ENERGY CONTENT: LECITHOTROPHIC DEVELOPMENT VERSUS PLANKTOTROPHIC DEVELOPMENT

A. INTRODUCTION

Fecundity and offspring quality (often indicated by egg size or energy content) that have been frequently used as indicators of parental fitness are believed to indicate reproductive success of an individual. Some life-history models have been developed based on the simplified assumptions that egg quality is positively related to egg size. Other models are based on the assumptions that egg size is correlated with the modes of development (planktotrophic versus lecithotrophic), the duration of larval life, and the survival of juveniles (Thorson 1946, 1950, Hermans 1966, 1979, Mileikovsky 1971, Vance 1973a, 1973b, Chia 1974, Schroeder and Hermans 1975, Strathmann 1977, 1980, Christiansen and Fenchel 1979, Caswell 1981, 1982, Grahame and Branch 1985). Although these models have been in existence for some years, two major aspects need to be addressed: (1) the role of environment in determining fecundity and offspring quality; and (2) the use of egg size as an indicator of mode of development, larval life span, and egg energy content (McGinley *et al.* 1987, McEdward and Carson 1987, McEdward and Coulter 1987).

It is believed that an increase in the amount of energy allocated to each offspring is likely to increase the fitness of that individual, but results in a concomitant decrease in fecundity (Lack 1954, Smith and Fretwell 1974, Lloyd 1987, McGinley *et al.* 1987, Winkler and Willin 1987).

Capitella sp. isan ideal species to examine the relationship between egg size and fecundity because in the same population of *Capitella* at the mudflat in Grappler Inlet, some individuals produce small eggs (125 μm in diameter) that develop into

planktotrophic trochophores and hatch from the adult tube within about one week, and others produce large eggs (250-400 μm in diameter) that develop within the tube of the adult worms into lecithotrophic larvae (See details in Chapter III).

Previous studies on the population dynamics of *C. capitata* have indicated that both the density and distribution of *Capitella* fluctuate dramatically, which is mainly dependent on the availability of food in the habitat, especially the absolute amount of nitrogen in the diet (Tenore 1975, 1977a, 1977b, Tenore *et al.* 1979, Alongi and Tenore 1985, Tenore and Chesney 1985, Tsutsumi 1987, Warren 1977). There is little evidence, however, to show how food quality affects the reproduction of *C. capitata* .

In this chapter,I attempt to address the following questions: (1) Does diet affect the growth and survival of either group of *Capitella* (lecithotrophic or planktotrophic developers)? (2) Does diet type influence the fecundity, generation time and time of sexual maturity of either group? (3) Does diet type affect the size and energy content of eggs? and (4) Does *Capitella* with either lecithotrophic or planktotrophic development have a similar response to the same type of diet ?

B. MATERIALS AND METHODS

1. Experimental designs

All animals used in this experiment were derived from individuals collected from a mudflat in Grappler Inlet near the Bamfield Marine Station, on the west coast of Vancouver Island, British Columbia. Plastic culture tray (length x width x height: 15 cm x 15 cm x 15 cm) was constructed with 50 μm mesh vents (vents were above the surface of sediment) on each wall and was provided with 5-7 cm thick layer of treated sediment. A total of 12 trays were used for lecithotrophic developers. The trays were placed in an seawater table with continuously flowing filtered (50 μm) seawater, and submerged in a 12 cm deep seawater table. Thirty five newly-emerged sibling juveniles were placed in each plastic tray and the 12 trays (contained 420 siblings in total) were divided into 4

groups. Each group (consisting of 3 trays and 105 juveniles in total) was provided with one type of diet (Fig. VI-1). Food was added to each tray daily at 2 mg dry weight/worm/day and later changed to 3 mg when the worms became adults. The sediment was replaced every two weeks. Prior to the addition of food, the seawater flow to the trays was stopped temporarily to allow pre-weighed food to be deposited on to the surface of the sediment. The temperature varied from 9-11°C throughout the experiments.

For the planktotrophic developing *Capitella*, another 12 trays were divided into 4 groups, each group also consisted of 105 newly-settled sibling juveniles and was provided with one type of diet (Fig. VI-1). The trays were maintained under the same conditions as described for lecithotrophic developers until animals were ready to spawn. Animals and sediment in each tray were then carefully transferred to a 1-liter culture beaker. The purpose of switching culture containers is to prevent loss of larvae when trochophores hatched during the period between two observations (interval was 7 days). The water in each beaker was changed daily by gently drawing it off through a Nitex mesh (20 μm) and replacing it with 50 μm filtered seawater.

2. Sediment preparation

Sediment was collected from the adult habitat, an intertidal mudflat in Grappler Inlet, in August 1987. Sediment was sieved through a 200 μm mesh sieve to remove large particles and then rinsed with tap water for at least 24 hrs to kill the remaining organisms (e.g., larvae and juveniles). The sediment was air-dried, and then stored in plastic bags for future use.

3. Diet preparation

Fresh *Ulva lactuca* and *Zostera marina* were collected from the intertidal zone in Grappler Inlet on August 17, 1987. *Nereocystis luetkeanā* and *Macrocystis integrifolia* blades were collected from the subtidal seaweed beds around the Bamfield Marine Station on August 21, 1987. Each plant was washed in seawater and then quickly rinsed with

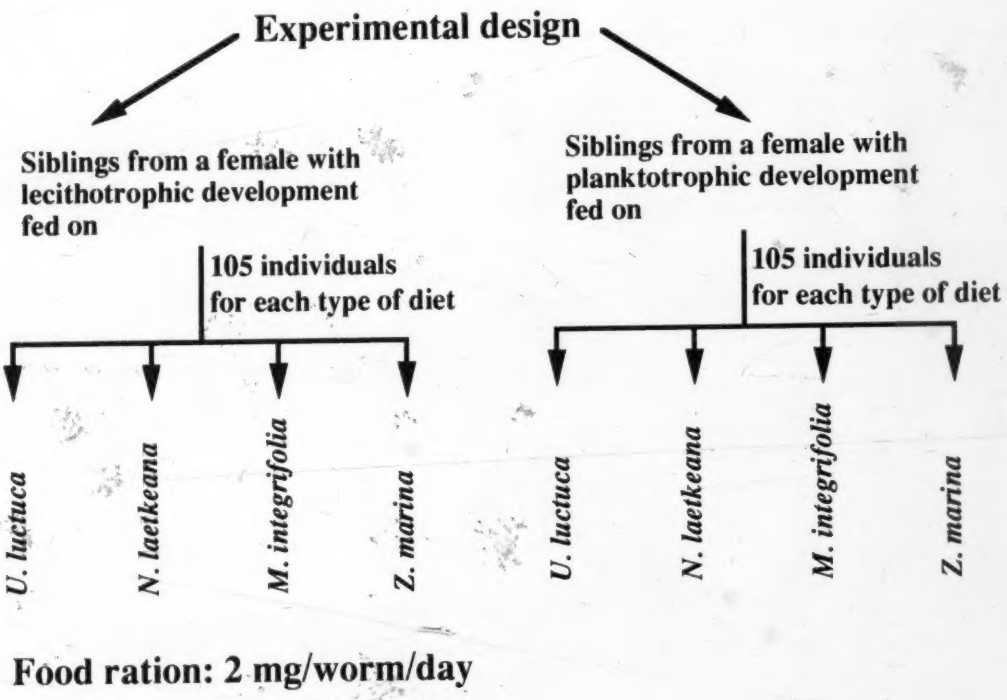

Figure VI-1: Outline of experimental design for experiments assessing the effects of diet type on growth and reproduction of both lecithotrophic and planktotrophic developers of *Capitella* sp.

tap water. After freeze-drying, the plants were ground with an electric mill, and then sieved through a 50 μm plastic screen. Food was stored in plastic bags until needed.

The carbon (C), hydrogen (H) and nitrogen (N) composition of each plant was measured in a C-H-N analyzer (Perlin-Elmer Model 240 analyzer) in the Department of Chemistry at the University of Alberta. Approximately 3-5 mg of the prepared diet were used for each measurement of elemental composition. Energy content (E, in joules, J) was calculated from the biochemical constituents (factors given by Winberg 1971): 23.64J/mg protein, 17.15J/mg carbohydrate, and 39.54 J/mg lipid. Total lipid content (Y) was estimated from (C) (i.e. X) by the following exponential equation: $\mathbf{Y=1.588\ X^{0.7015}}$ (Anger *et al.* 1983). Protein was estimated from (N) by multiplying N with the constant 6.25. Carbohydrate (Y) was calculated from (C) (ie. X) using the exponential equation: $\mathbf{Y=0.160\ X^{0.7193}}$ (Anger 1986).

4. Survivorship

To determine survivorship over time, the contents of each tray (animals and sediment) were transferred to a large dissecting pan. The individuals remaining were counted under magnification (16X) and then were returned to their original culture tray. Survivorship was calculated at two-week intervals and determined as the percentage of the original number of *Capitella*.

5. Growth

Growth rates were estimated by examining the changes in body length, diameter at the fifth setiger, body volume, and number of setigers at two-week interval over a 6 month period. These measurements were employed since it was impossible to determine the dry weight of animals without sacrificing them. Wet weight was not used in this study because an animal's gut contents will affect the accuracy of this measurement.

To measure the growth rates of *Capitella* that were fed on different types of food, body size and number of setigerous segments were calculated for a subset of five individuals randomly sampled from each tray every 2 weeks until the animals began to

reproduce (after 2.5 months for planktotrophic developers and 4 months for lecithotrophic developers). Each worm selected was transferred with its tube to a culture dish containing a small amount of seawater until it had crawled out of its tube. Animals without their tubes were relaxed with 0.36 M $MgCl_2$, and measured under a dissecting microscope with an ocular micrometer. The number of setigerous segments was also recorded for each individual. After the measurement had been taken, animals were immediately returned to the original culture tray. There was no significant effect of relaxation on an animal's survival in this experiment. Body volume (V) of each individual was calculated by the following equation: $V=\pi(D/2)^2 L$, where D and L are the diameter (width) and length of each worm. Growth rate (G) (net daily increase of body volume) and specific growth rates (G') (proportional increase in body volume) were determined by following the methods outlined in Chapter V.

Body length, width, and number of setigers were recorded for all worms again at the end of each experiment. The wet weight (WW) of each worm was determined after defecation had occurred; then the worms were dried at 100°C for 24 hrs for measurement of dry weights (DW). The relationships between body size and DW and between body size and WW were determined by regression analyses. It was found that the regressions between body volume and dry weight were highly significant for animals with either type of developments, indicating the body volume was a valuable indicator of an animal's mass.

6. Sex ratio

Sex of each individual was identified by examining the external sexual structures or visible ovaries. The percentages of males, females, and hermaphrodites in each tray were calculated, and then averaged to obtain data for the whole treatment group.

7. Fecundity

The fecundity of planktotrophic developers was recorded as the number of offspring per spawn, the number of spawns per female in each reproductive month, the

number of eggs per female in each reproductive month, and the total number of eggs produced in a female life-time. The fecundity of lecithotrophic developers was defined as the number of eggs produced in its first spawn, and these "females" may be real females or "morphological females". In order to count the eggs, once a worm began to release its eggs into the tube, the worm was removed from the culture tray and transferred to a beaker. After all the eggs were released into the tube, the worm was gently removed from the tube and returned to the original culture tray. The tube was then carefully opened with fine dissecting needles under a dissecting microscope and all the eggs were counted. The life-time fecundity of these individuals was not determined in this study.

8. Egg size

For each spawn, 20 to 30 newly-released eggs were measured (long axis and short axis) under a compound microscope. The egg volume (**V**) was determined by the following equation: $V=(4/3)\pi A^2 B$, where **A** and **B** are the radii of short and long axes of the egg, respectively.

9. Energy content in the egg

Energy content of the eggs was measured by dichromate oxidation against a glucose standard (0-300μg) by a modified procedure described by Parsons *et al.* (1984). Three replicates were used for each individual female, each replicate containing either 50 or 300 newly-released eggs (lecithotrophic and planktotrophic developers respectively). Details of the method were given in Chapter III.

10. Data analyses

Statistical comparisons of growth rates were made with ANCOVA and Student-Newman-Keuls multiple comparisons test (Sokal and Rohlf 1981, Zar 1984). The ANCOVA was used to determine whether diet type affected the slope or elevation of the growth and survival rate over the experimental times. If a significant effect was detected, Tukey multiple comparisons test was employed to separate the pairs of treatments which are actually differed.

Kruskal-Wallis tests and non-parametric multiple comparison tests were used to test the difference of biochemical constituents and CHN components in four food types, and to test the effects of diet type on sex ratio, sex maturation, spawning frequency of animals. One-way ANOVAs and Student-Newman-Keuls multiple comparison test were used to assess the effects of diet type on fecundity, egg size, egg energy content, and egg energy density (SPSS package, 1985). All statistical tests were applied at the 5% significance level.

C. RESULTS

1. Composition of diets

The elemental composition and biochemical constituents of *N. luetkeana*, *M. integrifolia*, *Z. marina*, and *U. lactuca* are listed in Table VI-1. The amount of nitrogen in *U. lactuca* was the highest among four food types while *M. integrifolia* contained the least. *Z. marina* and *N. luetkeana* contained similar and intermediate amounts of nitrogen. *U. lactuca* and *N. luetkeana* contained the greatest amount of carbon and hydrogen, while *M. integrifolia* contained the least. The caloric value decreased with food types as follows: *U. lactuca* = *N. luetkeana* > *Z. marina* > *M. integrifolia*. The differences in the amounts of protein, lipid, and carbohydrates among food types were also significant as they were calculated from the amounts of nitrogen and carbon of these sea plants. In conclusion, it appears that *U. lactuca* and *N. luetkeana* are the better food.

2. Lecithotrophic development

a. Effect of diet on growth

Sibling individuals of *Capitella* sp. raised on the four different diets showed significant differences in growth (Fig. VI-2A and B). When the changes in body volume over time were compared, the growth rates of *Capitella* sp. decreased with the diet types as follows: *U. lactuca* > *N. luetkeana* > *M. integrifolia* > *Z. marina*. Diet types also affected the changes in the number of setigers, however, did not affect the total number of

Table VI-1: CHN composition and estimated gross biochemical composition of *Nereocystis luetkeana, Macrocystis integrifolia, Ulva lactuca*, and *Zostera marina*. Carbon (C), nitrogen (N), hydrogen (H) are listed as percentage of dry weight. Energy content (E) was calculated as joule per dried, ground plant. Values represent the arithmetic mean and standard deviation, for five samples from each alga. Differences in all parameters were evaluated using Kruskal-Wallis test and the nonparametric multiple range test at 0.05 level.

	Ulva (U)	*Nereocystis*(N)	*Zostera* (Z)	*Macrocystis*(M)	Difference
C(%)	29.93±0.41	29.25±0.18	23.61±0.44	19.54±1.47	U N Z M
N(%)	3.44±0.10	2.70±0.05	2.64±0.18	2.13±0.15	N Z U M
H(%)	4.38±0.11	4.46±0.14	3.65±0.24	2.95±0.22	U N Z M
C/N	8.69±0.32	10.82±0.21	8.97±0.45	8.96±0.43	N U Z M
C/H	6.83±0.22	6.57±0.21	6.49±0.38	6.62±0.10	U N Z M
J/mg	11.67±0.16	11.41±0.07	9.21±0.18	7.63±0.58	U N Z M
Protein(mg)/mg	0.215±0.006	0.169±0.003	0.165±0.011	0.133±0.009	N Z U M
Lipid(mg)/mg	0.172±0.002	0.170±0.001	0.146±0.002	0.128±0.007	U N Z M
Carbon (mg)/mg	0.019±0.0	0.018±0.0	0.019±0.0	0.014± 0.0	U N Z M

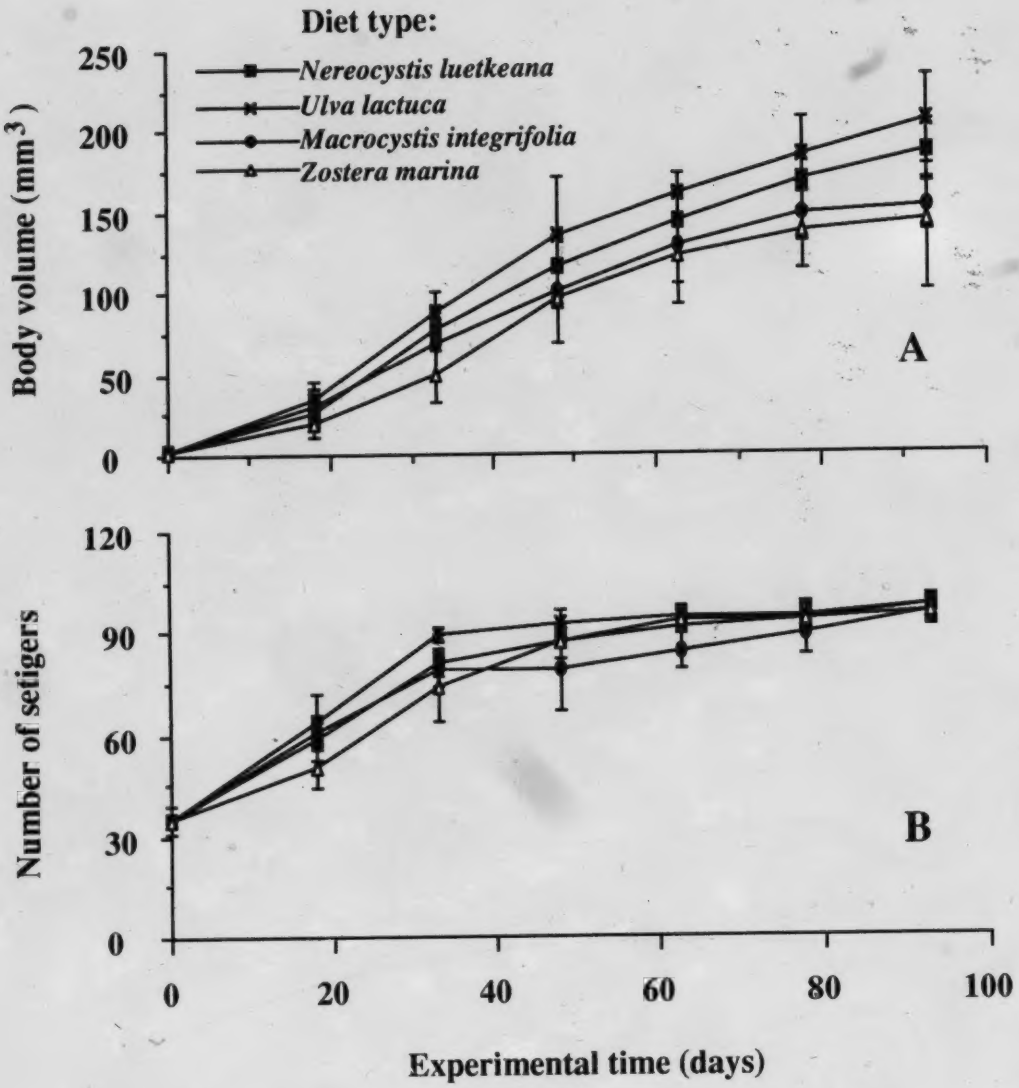

Figure VI-2: Effects of diet type on growth of *Capitella* sp. with lecithotrophic development: A, body volume; and B, number of setigers. Values plotted are mean ± standard deviation from measurement of fifteen animals.

Table VI-2: Least square linear regression equations for body volume and number of setigers over time (day 18-93) of *Capitella* sp. with lecithotrophic development. Results of an ANCOVA and Tukey multiple comparisons test comparing regressions among the groups fed on different diets are also shown. **U.**, *Ulva lactuca;* **N.**, *Nereocystis luetkeana;* **M.**, *Macrocystis integrifolia;* **Z.**, *Zostera marina*

	Regression		ANCOVA			Tukey test
Diet type	Equation equation	R^2		F	P	
		Body Volume				
U.	Y=2.83 + 2.10 X	0.98	Slope	1.95	>0.05	
N.	Y=10.0 +2.23 X	0.98	Elevation	8.81	<0.05	**U>N>M>Z**
M.	Y=11.46 + 1.67 X	0.97				
Z.	Y=2.12 + 1.69 X	0.96				
		Number of setigers				
U.	Y=59.80 + 0.45 X	0.84	Slope	2.8	>0.01	
N.	Y=68.70 + 0.36 X	0.74	Elevation	11.2	<0.01	**U>N=M>Z**
M.	Y=59.02 + 0.40 X	0.85				
Z.	Y=52.69 + 0.54 X	0.86				

setigers at the end of experiment (Fig. VI-2B). The results of ANCOVAs comparing the linear regression of body size over a period from day 19 to day 93 for four diet types are summarized in Table VI-2. Animals raised on *U. lactuca* almost reached their maximum number of setigers within one month; while animals raised on *N. luetkeana* and *M. integrifolia* had lower increase in the number of setigers at early stages, but reached the maximum number within the first two months. Although animals raised on *Z. marina* had the lowest increase rate at early stages of the experiment, they continually increased setigers at a constant rate throughout a 3 month period.

Figure VI-3A shows the daily net change in body volume throughout the experimental period. The maximum growth rate for animals fed on *U. lactuca*, *N. luetkeana*, and *M. integrifolia* occurred between day 18 to 33, while the animals fed on *Z. marina* reached their maximum growth rate at day 48.

Figure VI-3B shows the specific growth rate. Clearly, the smaller the animals, the higher the growth rate. However, diet did not affect specific growth rate (% increase in body volume), and the slopes of the regression lines for 4 food types were not significantly different (ANCOVA, $P>0.05$ for both slopes and elevation).

b. Relationship between body size to body weight

Body size of worms (volume, length, and diameter) was significantly correlated with both dry weight and wet weight, but there was no significant relationship between weight and number of setigerous segments (Fig. VI-4: A-H, Table VI-3).

c. Survivorship

Diet type did not affect the survivorship in *Capitella* sp. (Fig. VI-5; ANCOVA, $P<0.05$ for either slope or elevation of survivorship curves). Mortality was fairly constant and very low over the experimental period.

d. Sex ratio

A striking feature was the absence of males in the culture trays. Most of the animals (over 300 in total) were "morphological females"; i.e., they had one pair of

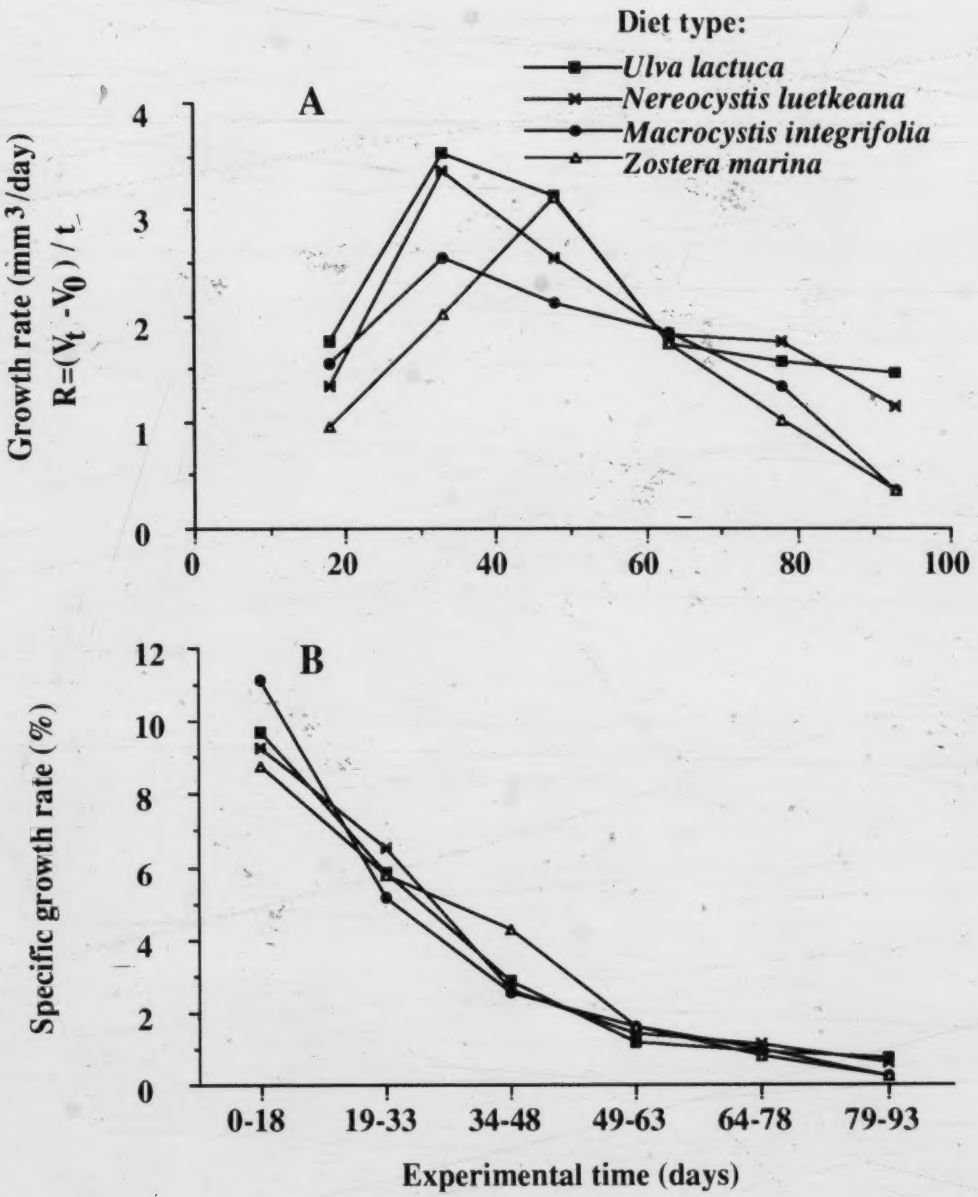

Figure VI-3: Effects of diet type on growth rate of *Capitella* sp. with lecithotrophic development. A, daily net change in body volume; B, specific growth rate (daily net change in body volume divided by mean value of body volumes at the beginning and the end of each interval).

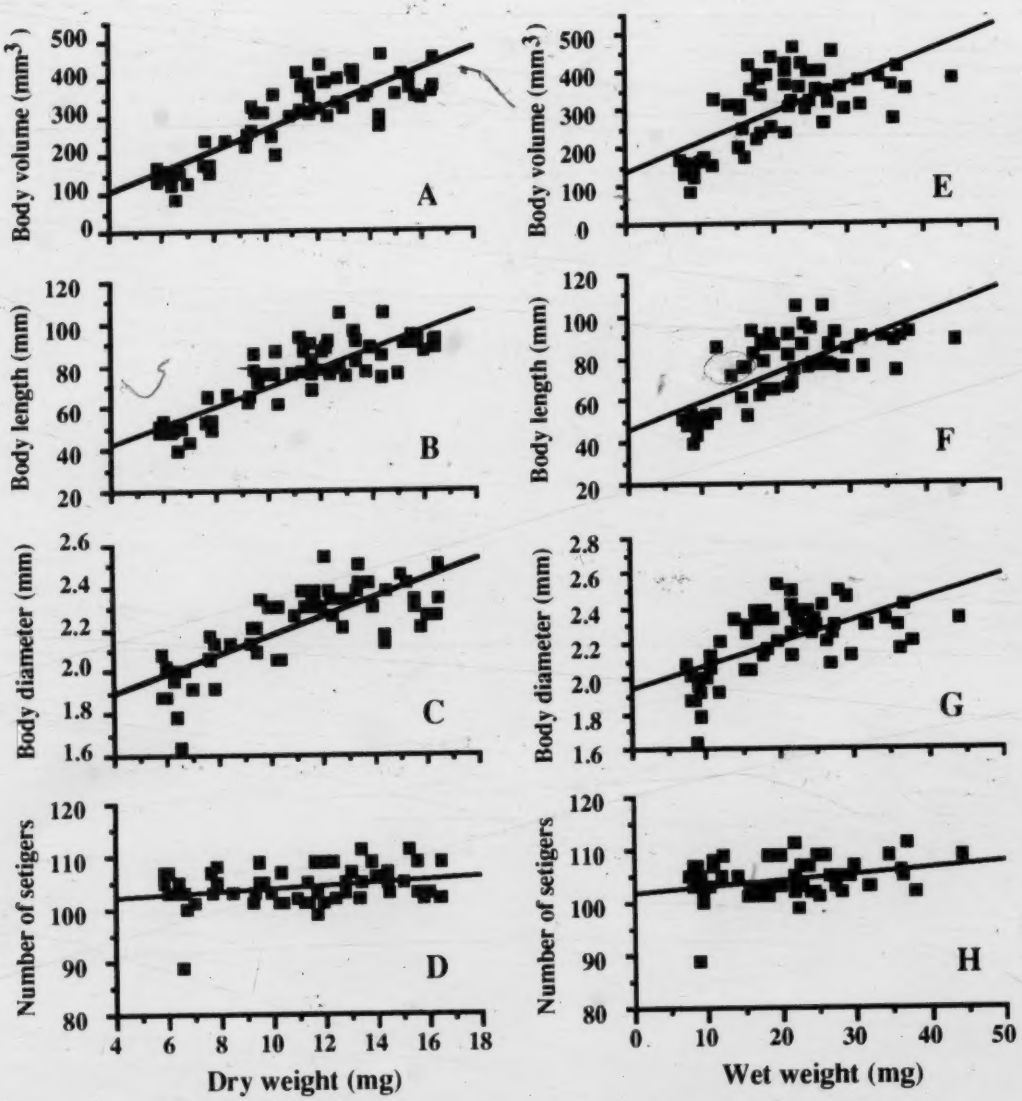

Figure VI-4: Relationship between body size and body weight of *Capitella* sp. with lecithotrophic development: A-D, relationship between body size and dry weight; E-H, relationship between body size and wet weight. Sample size is sixty.

Table VI-3: Least square linear regression equations for body volume, body length, body diameter, number of setigers versus dry weight and wet weight of *Capitella* sp. with lecithotrophic development. Results of one-way ANOVA are also shown.

Parameter (Y)	Regression equation	N	R	M. S.	F	P
	vs. dry weight (mg)(DW)					
Body volume	Y=-1.4 + 26.9x	60	0.86	446659	154.5	<0.0001
Body length	Y= 24.5 + 4.5x	60	0.85	12443	151.5	<0.0001
Body diameter	Y=1.7 + 0.05x	60	0.76	1.23	77.82	<0.0001
# of setigers	Y=101.4 + 0.3x	60	0.06	41.3	3.34	>0.05
	vs. wet weight (mg) (WW)					
Body volume	Y=135.4 + 7.8x	60	0.68	281285	48.6	<0.0001
Body length	Y= 46.1 + 1.4x	60	0.71	8547.7	56.8	<0.0001
Body diameter	Y=1.95 +0.01x	60	0.60	0.76	31.8	<0.0001
# of setigers	Y=10.2 + 0.11x	60	0.07	52.24	4.3	>0.05
DW vs WW	Y=-4.67 +2.28x	60	0.83	3209	128.6	<0.0001

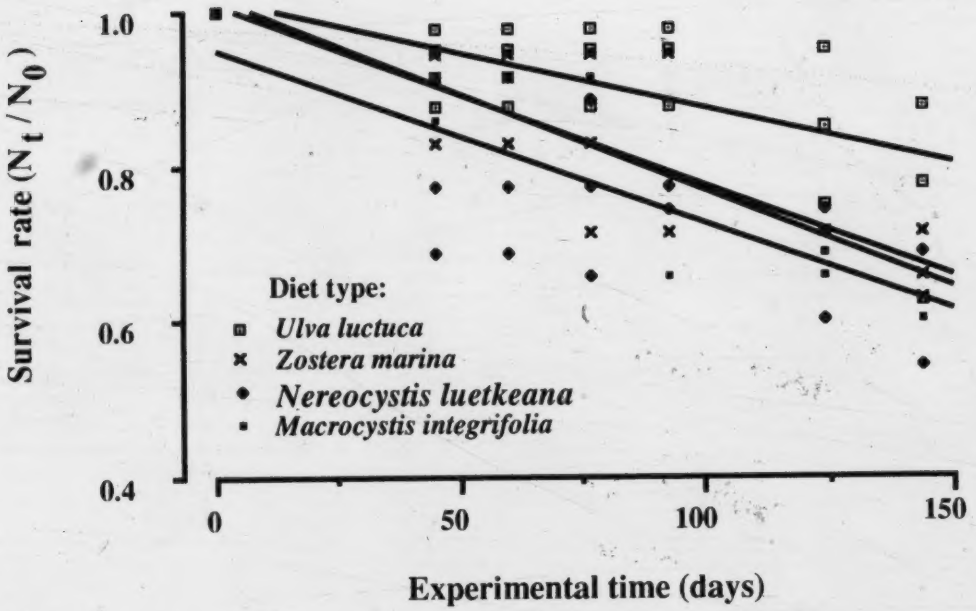

Figure VI-5: Effect of diet type on survival rate of *Capitella* sp. with lecithotrophic development.

ovaries in each fertile segment. Histological study demonstrated that these animals are hermaphrodites (Chapter VII) without copulatory spines--a characteristics separating males from females. A typical hermaphrodite in *Capitella* usually possesses both ovaries and copulation spines It was also found that diet type affected the number of typical hermaphrodites. About 17% of sexually mature individuals fed on *N. luetkeana* were morphological hermaphrodites; the animals fed on *M. integrifolia* and *Z. marina* contained 4% and 2% hermaphrodites respectively; and no morphological hermaphrodites were found among the individuals fed on *U. lactuca.*

e. Fecundity

Diet type affected the number of "morphological females" spawned within a given period (by the end of 4 months) (Kruskal-Wallis test, H=10.2, P=0.017 <0.05). Among the four groups, the individuals fed on *N. luetkeana* had the highest rate of spawning (99.25 ± 22.59%); and a significantly lower rate of spawning was found in all other groups: *Ulva* (75.45 ±1.65%), *M. integrifolia* (58.24 ±36.19%), and *Z. marina* (49.78±13.27%).

Fecundity (number of eggs shed in the first spawn of a individual) varied among the four diet groups (Table VI-4). Animals fed on *N. luetkeana* had the highest fecundity (X= 970 eggs/spawn); those fed on *U. lactuca* had a lower fecundity (X=827 eggs/spawn) although they had a larger body size than those fed on *N. luetkeana*; those fed on *M. integrifolia* had a mean fecundity of 713 eggs/spawn; and while those fed on *Zostera* had the lowest fecundity (X=594 eggs/spawn). In general, average fecundity was correlated with mean body size among the four groups (**Y= 1.196 X + 508.3, R=0.69, N=4; Y**: fecundity, **X**: body volume); however, this relationship was not significant within any one of those groups.

f. Egg size, egg energy content, and egg energy density

Egg sizes from worms fed on different types of diets were significantly different (Table VI-4). Although animals fed on *Z. marina* had the lowest fecundity, they

Table VI-4: Effects of diet type on fecundity, egg size,energy content and density of egg of lecithotrophic developing *Capitella* sp. with the results of one-way ANOVA and Student-Newman-Keuls multiple comparisons test among the diets. Values are mean ± standard deviation (sample size). Values that did not differ at the 0.05 level are joined by a solid line.

	Nereocystis (N)	*Macrocystis* (M)	*Ulva* (U)	*Zostera* (Z)	One-Way ANOVA F	P	Multiple Test 5%
Fecundity (eggs/spawn)	970±139 (59)	713±97 (48)	827±94 (55)	594±75 (42)	113.8	<0.0001	N M U Z
Egg volume	10.9±2.2 (920)	11.4±1.6 (620)	12.7±2.5 (780)	13.8±2.6 (520)	11.2	<0.0001	N M U Z
Egg long axis (µm)	293±27 (920)	303±23 (620)	311±21 (780)	316±23 (520)			
Egg short axis(µm)	265±18 (920)	267±13 (620)	277±21 (780)	287±20 (520)			
Microjoules/egg	69.8±14.4 (46)	77.6±10.5 (31)	79.6±10.1 (39)	88.5±5.46 (26)	14.98	<0.0001	N M U Z
Egg energy density	6.40±1.32 (46)	6.81±0.92 (31)	6.27±0.80 (39)	6.41±0.40 (26)	1.06	>>0.05	N M U Z

produced the largest eggs (13.77 x 10^{-3} mm^3) among the four groups, conversely, animals fed on *N. luetkeana* produced the smallest eggs while they had the highest fecundity (10.90 x 10^{-3} mm^3). A Student-Newman-Keuls (SNK) test showed that the sizes of the eggs produced by animals fed on *U. lactuca* and *Z. marina* were not significantly different; the sizes of the eggs produced by animals fed on *N. luetkeana* and *M. integrifolia* were also similar (Table VI-4), but differed significantly from those of the eggs produced by animals fed on *U. lactuca* and *Z. marina*. A SNK test indicates that the types of diets affected the egg energy content (Table VI-4): animals fed on *N. luetkeana* produced eggs with the lowest energy content (69.81 microjoules/egg); those fed on *Zostera* produced eggs with the highest energy content (88.53 microjoules/egg); whereas animals fed on *M. integrifolia* and *U. marina* produced eggs with a similar amount of energy which was intermediate between the other two groups. The differences in energy content per egg were simply the consequence of the differences in egg size among the groups, since the egg energy density did not differ among the four groups (Table VI-4).

3. Planktotrophic development

a. Effect of diet type on growth

Growth [body volume (A) and number of setigers (B)] of planktotrophic developing *Capitella* sp. over 4 months is shown in Fig. VI-6 A-B. The results of ANCOVAs comparing the linear regressions of body size over a period from day 15 to day 45 among the four types of diets are listed in Table VI-5, indicating that both body volume and number of setigers were significantly affected by the types of diets. Maximum growth was attained when fed with *U. lactuca* which was the major diet of *Capitella* sp. in the intertidal habitats. *N. luetkeana* also supported a comparatively good growth, but this is not a usual source of diet in the intertidal habitats. Neither *M. integrifolia* nor *Z. marina* provided a good growth rate. However, *Z. marina* is an important source of detritus in the intertidal habitat studied. Fragments of *M. integrifolia* were also found in the sediment associated with intertidal habitats of this species.

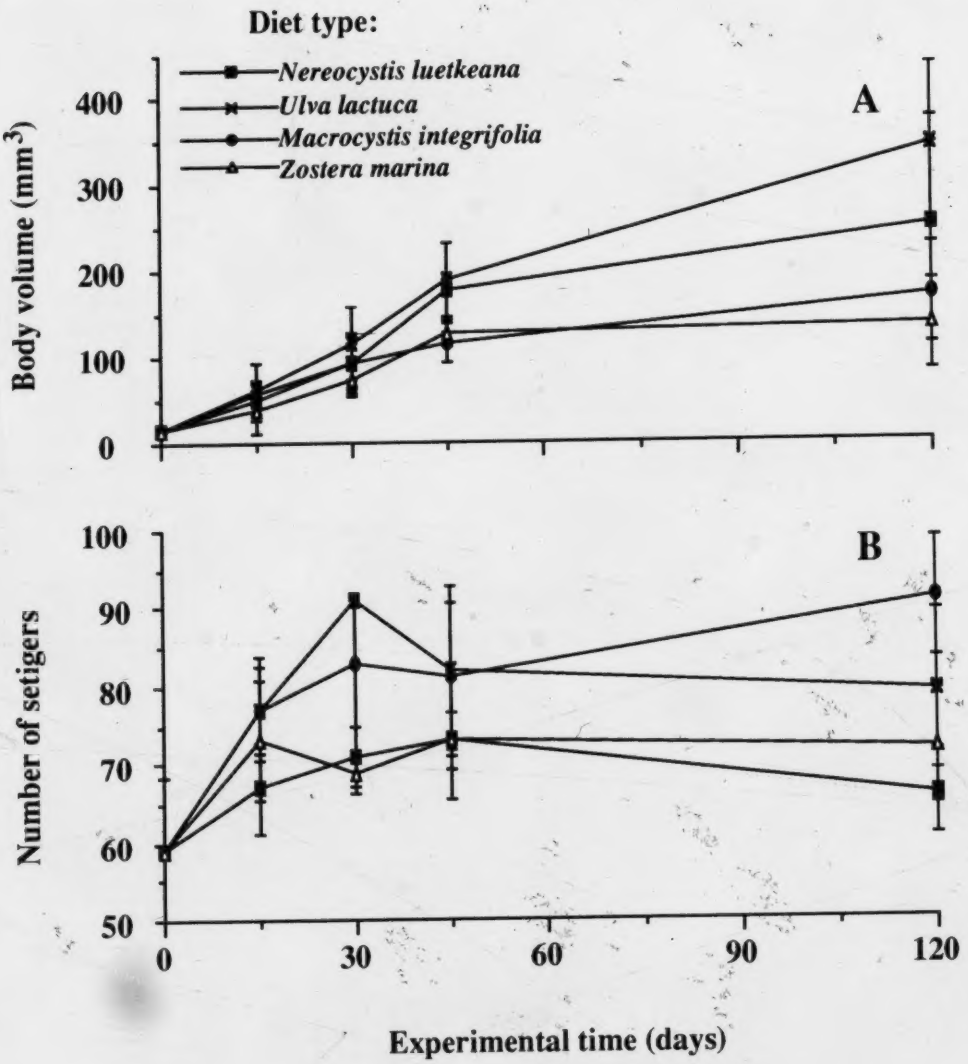

Figure VI-6: Effects of diet type on growth of *Capitella* sp. with planktotrophic development: A, body volume; and B, number of setigers. Values plotted are mean ± standard deviation from measurement of fifteen animals.

Table VI-5: Least square linear regression equations for body volume and number of setigers over time (day 15-45) of *Capitella* sp. with planktotrophic development. Results of an ANCOVA and Tukey multiple comparisons test comparing regressions among the groups fed on different diets are also shown. **U.**, *Ulva lactuca;* **N.**, *Nereocystis luetkeana;* **M.**, *Macrocystis integrifolia;* **Z.**, *Zostera marina*

	Regression		ANCOVA			Tukey test
Diet type	Equation equation	R^2		F	P	
		Body Volume				
U.	Y=-23.6 + 4.33 X	0.89	Slope	4.9	>0.05	
N.	Y=-4.19 + 4.20 X	0.97	Elevation	4.6	<0.05	**U>N>M=Z**
M.	Y=29.81 + 1.95 X	0.86				
Z.	Y=-11.35 + 3.0 X	0.71				
		Number of setigers				
U.	Y=64.33 + 0.20 X	0.89	Slope	2.81	>0.05	
N.	Y=69.33 + 0.47 X	0.91	Elevation	11.21	<0.01	**U=N>M=Z**
M.	Y=76.33 + 0.13 X	0.87				
Z.	Y=71.67 + 0.001X	0.78				

Figure VI-7A shows the net changes in body volume over the experimental period. Daily net growth increased in groups fed on *N. luetkeana*, *U. lactuca* and *Z. marina*, over the period of the first 6 weeks, just before the animals began to reproduce. Animals fed on *M. integrifolia*, however, had the highest net growth as juveniles, but the growth rate (daily net increase in body volume) declined with age.

Figure VI-7B shows the specific growth rate of worms of each diet group. Clearly, smaller animals had higher growth rate than larger animals. Diet type, however, did not affect specific-body volume growth rates, as slopes of the regression lines for the four diet types were not significantly different (ANCOVA, $F=1.65$, $P>0.01$; $F=1.42$, $P>0.05$ for slope and elevation respectively).

b. Relationship between body size and body weight

Body length, diameter, and volume were all correlated with dry weight and wet weight (Fig. VI-8, Table VI-6); but there was no significant relationship between body weight and number of setigerous segments (Fig. VI-8, Table VI-6).

c. Survivorship

Diet type did not affect the survivorship of *Capitella* sp. (Fig. VI-9; ANCOVA test: $F=1.04$, $P>0.05$ for slope; $F=1.33$, $P>0.05$ for elevation); this was because age-specific survivorship was highly variable. The highest mortality occurred at the age of 3.5 to 4 months and this may be related to reproductive activities. Over 80% of the experimental animals survived and reproduced 2 to 3 times before they died at about 4 months old. There was no apparent difference in the survivorship between males and females (T-test, $t=1.14$, $P>0.05$).

d. Mode of development and sex ratio

Out of 294 sexually matured individuals, eighteen of them (6.1%) became lecithotrophic developers. Four typical morphological hermaphrodites (1.3%) appeared in the experimental trays (1 with *U. lactuca*, 2 with *M. integrifolia*, 1 with *N. luetkeana*) and they are also lecithotrophic developers. The remaining 272 individuals were distinctive planktotrophic

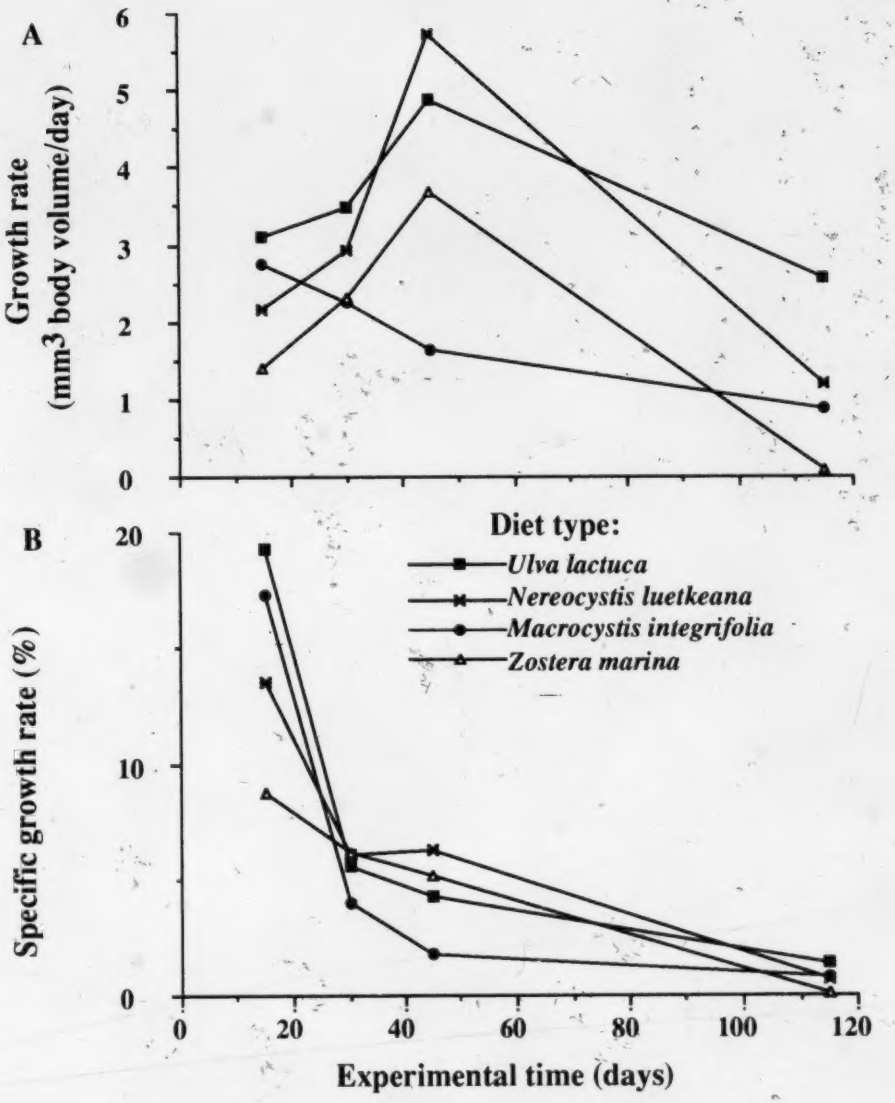

Figure VI-7: Effects of diet type on growth rate of *Capitella* sp. with planktotrophic development: A, daily net change in body volume; B, specific growth rate (daily net changes in body volume divided by mean values of body volumes at the beginning and the end of each interval).

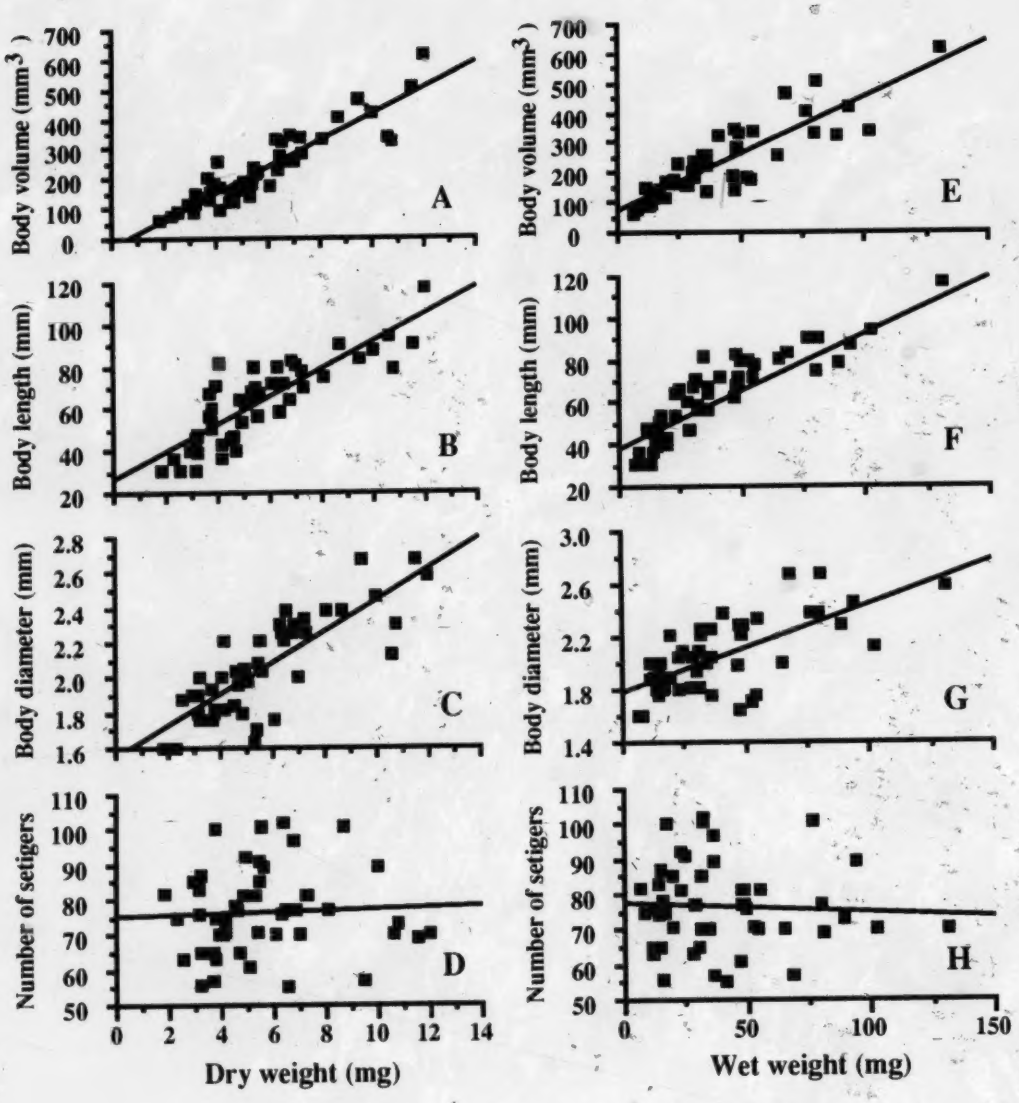

Figure VI-8: Relationship between body size and body weight of *Capitella* sp. With planktotrophic development: A-D, relationship between body size and dry weight; E-H, relationship between body size and wet weight. Sample size is fourty-eight.

Table VI-6: Least square linear regression equations for body volume, body length, body diameter, number of setigers versus dry weight and wet weight of *Capitella* sp. with planktotrophic development. Results of one-way ANOVA are also shown.

Parameter (Y)	Regression	N	R	M. S.	F	P
	vs. dry weight (mg)(DW)					
Body volume	Y=-26.1 + 44.4x	48	0.92	575741	255.1	<0.0001
Body length	Y= 26.4 + 6.5x	48	0.85	12440.4	115.4	<0.0001
Body diameter	Y=1.55 + 0.1x	48	0.81	2.33	88.5	<0.0001
# of setigers	Y=75.5 + 0.2x	48	0.00	12.6	0.08	0.78
	vs. wet weight (mg) (WW)					
Body volume	Y=71.1 + 3.8x	48	0.88	524285	155.4	<0.0001
Body length	Y= 38.4 + 0.6x	48	0.89	13793	175.9	<0.0001
Body diameter	Y=1.8 +0.01x	48	0.67	1.59	37.6	<0.0001
# of setigers	Y=77.8 - 2.8x	48	0.00	27.9	0.18	0.67
DW vs WW	Y=2.3 + 0.08x	48	0.93	254.1	301.9	<0.0001

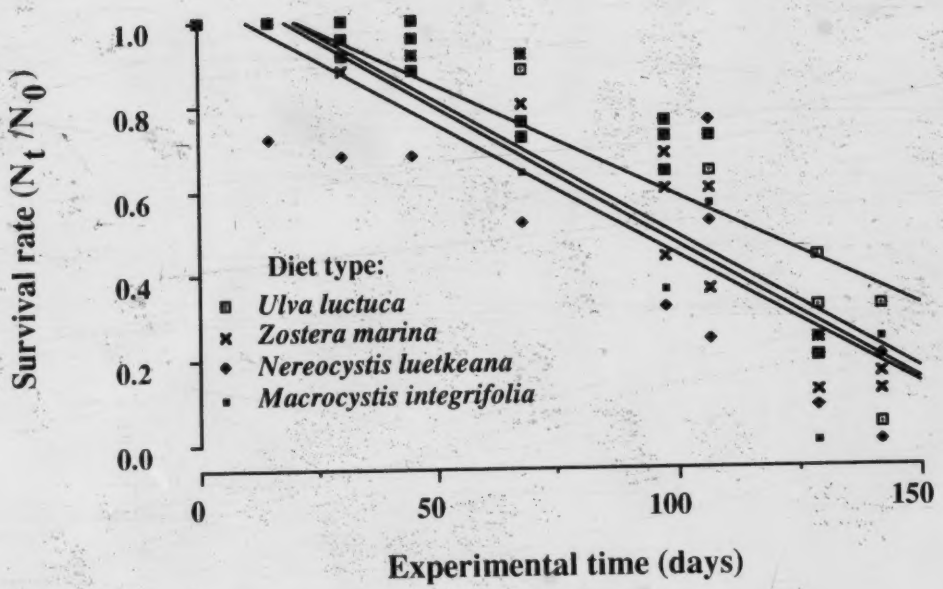

Figure VI-9: Effect of diet type on survival rate of *Capitella* sp. with planktotrophic development. Values plotted are the percentage of animals remained in each relicate culture at each interval .

developers, of which there were 146 females (53.68%) and 126 males (46.32%). Diet type significantly affected the proportion of gravid females (Fig. VI-10; Kruskal-Wallis test: H=9.43, P=0.024). Animals fed on *Z. marina* had a higher proportion of males (54.16%) than those fed on other diets; while animals fed on *U. lactuca* had a higher percentage of females (66.59%). The sex ratio of animals fed on *M. integrifolia* or *N. luetkeana* was close to one. A non-parametric multiple comparison test detected the differences only between *Zostera* and other three groups.

e. Fecundity

Animals fed on *Z. marina* reached sexual maturity sooner and also reproduced more frequently within the first 2 months than animals fed on other diets (month 1 refers to the month that the first animal began to reproduce) (Table VI-7). Animals fed on *N. luetkeana* reached sexual maturity slightly after those fed on *Zostera*, and had a lower frequencies of spawning within the "first two months" (Table VI-7). Animals fed on *U. lactuca* and *M. integrifolia* were the last to reach sexual maturity.

The number of eggs produced in a single spawn within each month was not significantly different among the four groups (Table VI-7). This was mainly due to the tremendous variations within each group. If the data in three successive months were pooled, the fecundity, calculated in terms of number of eggs per spawn, showed no difference among the four groups (Table VI-7). However, the life-time fecundity was higher in animals fed on *Z. marina* and *N. luetkeana* than those fed on *M. integrifolia* and *U. lactuca* (Table VI-7).

f. Egg size, egg energy content, and egg energy density

Egg volume was not affected by the types of diets (Table VI-7), which may have been caused by the large variations observed among-individuals within each group.

Diet type affected the egg energy content of eggs (Table VI-7). A SNK test revealed that the eggs produced by animals fed on *N. luetkeana* contained less energy compared to the eggs produced by animals fed on the other 3 types of diets; the animals

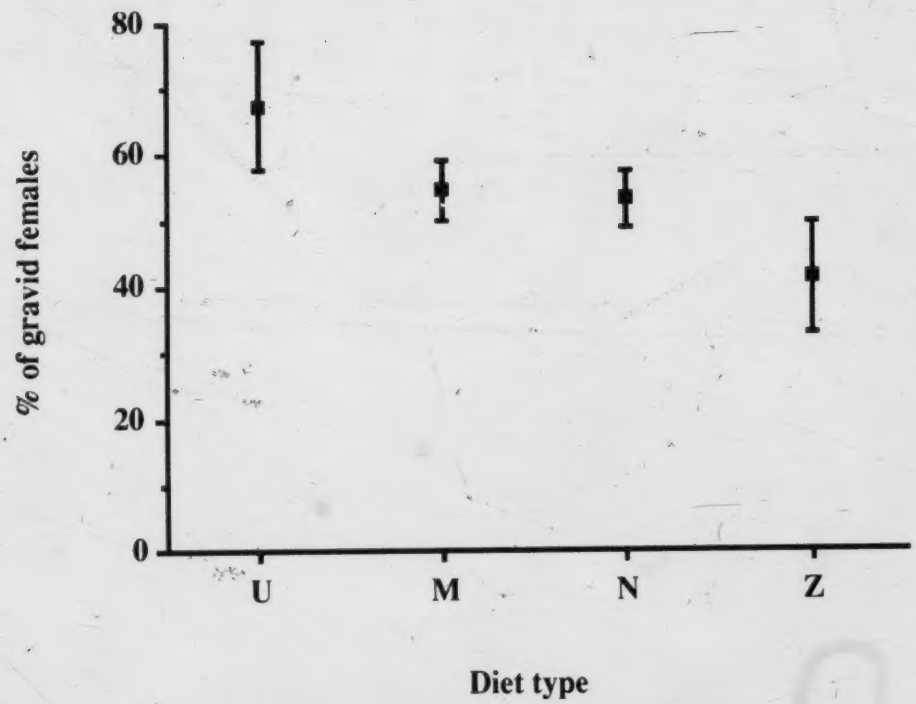

Figure VI-10: Effect of diet type on the proportion of gravid females in all females of *Capitella* sp. with planktotrophic development. Values plotted are mean ± standard deviation, for three replicate cultures. U, *Ulva lactuca*; M, *Macrocystis integrifolia*; N, *Nereocystis luetkeana*; Z, *Zostera marina*.

Table VI-7: Effects of diet type on fecundity, egg size, egg energy content and density of planktotrophic developing *Capitella* sp. with the results of one-way ANOVA and Student-Newman-Keuls multiple comparisons test among the diets. Values are mean ± standard deviation (sample size). * indicates that sample sizes are the number of replicate cultures, and statistical analyses were conducted with Kruskals-Wallis tests and nonparametric multiple comparisons tests. Values that did not differ at the 0.05 level are joined by a solid line.

	Nereocystis (N)	*Macrocystis* (M)	*Ulva* (U)	*Zostera* (Z)	One-Way ANOVA F	P	SNK Test 5%
Spawns/life-time*	4.5±0.8 (3)	2.6±1.1 (3)	3.0±1.0 (3)	4.8±0.6 (3)	4.4	<0.05	M U N Z
Spawns/1st M*	1.4±0.8 (3)	0.5±0.2 (3)	0.7±0.3 (3)	1.8±0.3 (3)	10.6	<0.05	N Z M U
Spawns/2nd M*	1.7±0.9 (3)	0.6±0.4 (3)	1.1±0.5 (3)	2.1±0.4, (3)	3.8	>0.05	N M U Z
Spawns/3rd M*	1.4±1.0 (3)	1.5±0.8 (3)	1.2±0.5 (3)	0.9±0.1 (3)	0.4	>>0.05	N M U Z
Eggs/spawn	2217±1490 (99)	2540±1420 (60)	2139±2124 (79)	2094±1358 (93)	1.0	>>0.05	N M U Z
Eggs/spawn/1st M	2117±1430 (45)	3152±1405 (19)	2918±3271 (26)	1895±1019 (48)	3.3	<0.05	M U N Z
Eggs/spawn/2nd M	2543±1595 (39)	2366±1134 (19)	2189±1123 (33)	2457±1597 (35)	0.4	>>0.05	N M U Z
Eggs/spawn/3rd M	1671±1258 (15)	2162±1534 (22)	1046±479 (20)	1776±1723 (10)	2.7	<0.05	M N Z U
Eggs/life-time	10058±2235	6796±2581	6387±2092	10205±1212			
Egg volume	1.07±0.22 (720)	1.09±0.27 (400)	1.13±0.26 (600)	1.2±0.2 (900)	1.93	>0.05	N M U Z
Miceojoules/egg	9.75±1.95 (36)	8.97±1.95 (20)	8.97±1.56 (30)	10.14±2.34 (45)	2.56	>0.05	N M U Z
Egg energy density	9.11±1.82 (36)	8.23±1.79 (20)	7.93±1.38 (30)	8.45±1.95 (45)	1.66	>0.05	N M U Z

from the later three groups produced the eggs with a similar energy content. Diet type did not affect the egg energy density either (Table VI-7).

4. Comparison of growth rate between animals with different developmental modes

Table VI-8 listed the results of ANCOVA of growth curves of animals with planktotrophic and lecithotrophic development fed each type of diet. Clearly, animals with planktotrophic development grew faster and reached sexual maturity sooner than those with lecithotrophic development when they fed on the same kind of diets.

D. DISCUSSION

1. Growth

Both laboratory experiments and field observations have indicated a positive relationship between individual or population growth and diet among the marine invertebrates (Crump 1971, MacDonald and Thompson 1985, 1986, Levin 1986, Zajac 1986, Marsh *et al.* 1989, Taghon and Greene 1990, Xu and Barker 1990, Qian and Chia 1991). With respect to *C. capitata*, many laboratory studies have demonstrated that population growth (density) can be mediated by food quality (Tenore 1975, 1977a, 1977b, Tenore *et al.* 1979, Tenore and Hanson 1980a, Tenore 1981, Tenore and Chesney 1985, Grémare *et al.* 1988, 1989a): the better the quality of diet, the higher the growth rate of the population. Individual growth of *Capitella* sp. I was dependent on the amount of nitrogen in the diet (Grémare *et al.* 1988). Further, Marsh *et al.* (1989) suggested that growth rates of juvenile *Capitella* sp. I were correlated with levels of the amino acids histidine, phenylalanine, threonine, and valine, and the polyunsaturated fatty acid 20:5w3. In this study, the individual growth rate is related to the type of diets that animal ingested, but there is no clear relationship between growth rate and amount of nitrogen in food.

Table VI-8: Summary of results from ANCOVAs comparing the change in body volume over time between planktotrophic and lecithotrophic *Capitella* sp. fed on the same type of diets.

Diet type	Adjusted means		Slopes		Common slope
	F-value	P-value	F-value	P-value	
Nereocystis	12.22	< 0.01	2.04	>0.01	0.74
Ulva	7.73	<0.05	1.42	>0.01	0.73
Macrocystis	22.63	<0.01	0.86	>0.01	0.61
Zostera	21.82	<0.01	3.23	>0.01	0.65

It has been well demonstrated that marine plants differ in their nutritive values (Carefoot 1967, 1973, Tenore 1975, 1977, Tenore *et al.* 1979, Tenore and Chesney 1985, Thompson 1985, Levin and Creed 1986, Zajac 1986, Grémare *et al.* 1988, 1989a, 1989b, Martel 1990). This was supported by the results of my study. In my study area, *U. lactuca* and *Z. marina* were probably the major sources of food for *Capitella*. Several previous studies have indicated that *U. lactuca* is a good food for *Aplysia punctata* (Carefoot 1967), *Triphneustes ventricosus* (Lilly 1975), and *C. capitata* (Grémare *et al.* 1988, 1989a) since it usually provides good growth. In fact, *Ulva* spp. are not only the major food sources for *C. capitata* populations over the world (Tenore 1975, 1977, Tsutsumi 1987, Grémare *et al.* 1988, Wu *et al.* 1988) but they were also commonly used as food for laboratory studies of *C. capitata* (Reish 1977). On the other hand, *Z. marina* is a nitrogen-poor flowering plant, and contains refractive structural carbohydrates that are decay-resistant, and has a very low growth-supporting value for *C. capitata* (Tenore 1977a, 1977b).

This is the first study to compare the growth rates of siblings with different developmental modes under similar laboratory conditions. Since the amount of food given to the experimental animals in both groups was the same, the differences should be considered due to genetic factors. It is noted that animals with planktotrophic development not only grew much faster but also reached sexual maturity quicker than lecithotrophic developers that fed on the same type of diet. These indicate that planktotrophic developers have a better capacity to convert food energy into growth of somatic and gonadal tissue than that of lecithotrophic developers.

2. Reproduction

a. Spawning

Both food type and ration can influence the proportion of breeding individuals in a population. Grémare *et al.* (1989a, 1989b) found that in *C. capitata* type I, the proportion of gravid females was significantly greater in groups fed on *Ulva* than in

groups fed on diatoms or Tetramen, whereas the proportion of gravid females was greater in groups fed on *Ulva* and diatoms than in those fed on Tetramen. In my study, planktotrophic developers fed on *Z. marina* reached sexual maturity earliest among the four diet groups although *Z. marina* provided the poorest growth rate to *Capitella*. Animals fed on *Z. marina* also spawned more times than those fed on *U. lactuca* and *M. integrifolia* within the first two reproductive months. In contrast, although animals fed on *U. lactuca* had the highest growth rate among the four diets, they did not spawn as frequently as those fed on *Z. marina* within a given period. In lecithotrophic developers, although animals fed on different diets showed different growth rates, they reached sexual maturity (indicated by spawning) at the same age, indicating that diet type did not affect the timing of spawning in these individuals. These results indicate that 1) lecithotrophic and planktotrophic developers have different response to their diet in terms of both growth and reproduction; and 2) food which is good for an animal's somatic growth may not be good for the growth of reproductive tissues, which means reproduction and growth may require different food components.

b. Fecundity

Numerous reports have demonstrated that diet and ration can ultimately determine the fecundity in marine invertebrates (Bayne *et al.* 1978, 1980, 1983, McKillup and Butler 1979, Thompson 1982, Lewis and Storey 1984, MacDonald and Thompson 1985, 1986, Ohamart *et al.* 1985, Levin and Creed 1986, Zajac 1986, Levin *et al.* 1987, Barber *et al.* 1988, Grémare *et al.* 1988, 1989a, 1989b, Verity and Smada 1989, White and Dagg 1989, Martel 1990) and in vertebrates (Lack 1967, Bengston 1971, Kuznetsov 1973, Krapu 1979, Duncan 1986, Kaev and Kaeva 1987, Henrich 1988, Boag 1989). These studies indicate that the number of offspring is affected not only by the parental investment in each offspring, but also by the total resources available to the parents, and the fraction of these resources devoted to reproduction. Since most of the reported results are based on observations of wild populations from different habitats or from

different reproductive seasons, it is difficult to assess whether or not the differences are genetically or environmentally based. In this study, I found that diet type has significant effects on the number of eggs produced in the first spawn of lecithotrophic development as individuals fed on *Nereocystis* produced almost twice as many eggs as those fed on *Zostera*. Also, diet type affected the numbers of spawns, age of spawn, and life-time fecundity of planktotrophic developers. Although there are great variations in the numbers of spawns, number of eggs per spawn among siblings of planktotrophic developers that fed on the same food, the life-time fecundity was significantly different among groups. Animals fed on *Z. marina* and *N. luetkeana* were more fecund than those fed on *U. lactuca* and *M. integrifolia*. On the other hand, animals fed on the same diets showed limited variations among sibling individuals of lecithotrophic development, indicating that there is limited variations among these siblings. In contrast, greater variations in fecundity has been recorded in this study among the siblings of planktotrophic developers, as sibling individuals that fed on the same diet showed great differences in fecundity. These results suggest that variations existing among siblings derived from a single spawn of planktotrophic developers are greater than the variations existing among the siblings of lecithotrophic developers. This further implies that planktotrophic developers are more adaptable to a dynamic environment than lecithotrophic developers.

In previous studies, fecundity has been defined as 1) the number of eggs produced by single animal in single spawn, 2) the number of eggs found within animal's body, 3) the dry weight or wet weight of gonads, or 4) the total number of eggs produced during the life-time of an animal. In this study, fecundity was expressed in both (1) and (4).

No relationship was established between body size and fecundity for planktotrophic developers either within a group or among groups. For lecithotrophic

developers, the relationships between body size and fecundity existed only among the groups.

c. Egg size

In marine invertebrates, egg size has been reported to change with reproductive season, temperature, habitats, and food supply (Kerfoot 1974 , Barnes and Barnes 1965, Bayne *et al.*, 1975, Bayne *et al.* 1978, Turner and Lawrence 1979, Brambilla 1982, Thompson 1982, Berglund 1984). Egg size is also known to change with diet type and other environmental conditions in insects (Capinera 1979, Ohmart *et al.* 1985) and isopods (Brody and Lawlor 1984). Proximate factors known to affect egg size in various species of fish are female size (Kuznetsov 1973, Kaev and Kaeva 1987), female age (Lee 1981, Kuznetsov 1983), timing of spawning season (Bagenal 1969, 1971), food availability (Bagenal 1971, Boag 1989) or temperature and salinity (Lee 1981). In birds, egg size varies with female age (Davis 1975, Brooke 1978, Furness 1983), female body size (Festing and Nordskog 1967, Grant 1982, Lomen 1984), laying date (Coulson *et al.* 1969, Parsons 1972, Runde and Barrett 1981, Furness 1983), and diet types (Krapu 1979, Sharp and Moss 1981, Beckerton and Middleton 1982, Duncan 1986). There are also a few studies that describe variation of egg size in amphibians (Crump and Kaplan 1979, Kaplan 1980a, 1980b, Crump 1981, Kaplan and Cooper 1984). However, since most of these studies dealt with comparisons of different populations, different breeding seasons, or different species, it is very difficult to define how much these variations are due to a given environmental factor. In this study, since sibling individuals were used and only one environmental variable (diet type) was introduced, the variation in egg size is likely due to genetic difference among siblings fed on the same type of diets, and that the variation among the groups (fed on different diets) should be the results of the differences of diet type. It was found that the differences among siblings within each groups introduce about 20% variation (this was calculated by dividing each standard deviation by its mean egg volume) in egg size for either

planktotrophic or lecithotrophic developers. Diet type did not have significant effect on the egg size of planktotrophic developers, but it affected the egg size of lecithotrophic developers.

This is the first study to compare the reproduction of siblings with different developmental modes. In general, the planktotrophic developer is more flexible than the lecithotrophic developer because it has higher variations among the siblings. Indeed, the offspring of a planktotrophic developers showed very high plasticity in reproductive characteristics. Previously, I have shown that when fed on squid egg capsules, these worms produced five to seven times more eggs than their siblings fed on ground seaweed and their eggs were also significantly smaller (Chapter V). Experiments described here are also the first conducted under controlled conditions to examine the relationship between body size and egg size among the siblings. The egg size of planktotrophic developers was not affected by adult body size; but the egg size of lecithotrophic developers was inversely related to body size.

d. Egg energy content

This study provides evidence to show that there is an inverse relationship between fecundity and egg size in *Capitella*. Lecithotrophic developers fed on *Z. marina* had the lowest fecundity but had the largest egg and, on the other hand, those fed on *N. luetkeana* had the highest fecundity but had the smallest egg. It has been recognized that an increase in egg size or egg quality is likely to increase the survival rate of offspring among the vertebrates such as in fish (Blaxter and Hempel, 1963, Blaxter 1969, Bagenal 1969, Marsh 1984, 1986, Henrich 1988), amphibians (Kaplan 1980a, 1980b, Kaplan and Cooper 1984), and birds (Furness 1983, Duncan 1986). The increase in egg size may also increase the size of larvae or juveniles at hatching time of salamanders *Ambystoma* spp., and organgethroat darter, *Etheostoma spectabile* (Kaplan 1980a, 1980b, Kaplan and Cooper 1984, Marsh 1986), or shorten the larval life span of salamanders (Kaplan and Cooper 1984). Although the relationship between egg size and

survival rate of offspring has not been as well studied in marine invertebrates as in vertebrates, Kraeuter *et al.* (1982) found that in the hard clam, *Mercenaria mercenaria*, and bay scallop, *Argopecten irradians*, larger eggs developed into larger larvae with a better survival rate. It has also been suggested that larger eggs with high energy content may have higher fitness in terms of mortality rate of embryos and larvae, or duration of development than smaller eggs with less organic material among the echinoids (McEdward 1986).

In a recent study, Marsh *et al.* (1990), found that diet types affected oocyte yolk-composition (fatty acids and sterols) in *Capitella* sp. I. In my study, I also found that diet affected egg energy content of lecithotrophic developers. These results suggest that diet can affect the quality of egg, in turn, it may influence larval growth and development.

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CHAPTER VII

THE "MORPHOLOGICAL FEMALES" ARE FUNCTIONAL HERMAPHRODITES

A. INTRODUCTION

All sibling species of *Capitella capitata* reported so far have separate sexes, with only males or hermaphrodites possessing copulating spines and those without copulatory spines and containing visible ovarian structures being considered females. The term "Morphological female" was proposed by Eckelbarger and Grassle (1987), referring to the individuals of *Capitella* raised in isolation from juveniles that had no copulating spines, but can produce fertilized eggs and viable larvae.

In this chapter I confirm the findings of Eckelbarger and Grassle (1987) and provide morphological evidence to show that the so-called "morphological females" are in fact functional hermaphrodites. I further report that sperm development in this species takes place either in the wall of the coelomoducts or in the coelom.

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Qian, Pei-Yuan and Fu-Shiang Chia, The "morphological females" of a marine polychaete, *Capitella* sp., are the functional females. Mar. Biol., (Submitted)

B. MATERIALS AND METHODS

Adults of *Capitella* sp. were collected from an intertidal mudflat in Grappler Inlet, Bamfield, British Columbia, Canada. These individuals produced large eggs that developed into lecithotrophic larvae. Larvae developed in the adult tube into either juveniles crawling out of the tube or into 13-15 setigerous larvae that emerged from the tube and swam in the water for 24 hours prior to settling. The details of life-history characteristics have been described in Chapter III of this thesis. In the laboratory, 100% of juveniles reared either in isolation or at a high density (>2000 worms/m^2) developed into "morphological females".

To determine the sex of these animals in the laboratory, sibling juveniles of *Capitella* sp. right after hatching, were isolated individually into separate culture beakers, and each animal was provided with sediment that was collected from the mudflat in Bamfield Inlet, British Columbia. The sediment was freeze-dried, stored in plastic bags, and then shipped to Edmonton. Prior to being added to each culture beaker, the sediment was heated in an oven at 120°C for 12 hours. Animals were fed with ground *Ulva*. Each culture beaker was provided with seawater (instant ocean seawater system) and maintained at 10± 1°C in marine aquaria room in the Department of Zoology, University of Alberta.

Prior to fixation, the worms were anesthetized in equal parts of isotonic $MgCl_2$. For histological studies, anesthetized worms of different stages were fixed in Bouin's solution for 24 hours, and then washed with 50% ethanol for several times prior to be transferred into 70% ethanol with NH_4 (<1 drop/50 ml ethanol). The worms were dehydrated using a Fisher Histomatic Tissue Processor Model 166 (70% ethanol, 90% ethanol, 100% ethanol, 100% ethanol, 100% toluene:100% ethanol, each for one hour; then double changes in 100% toluene, half hour for each change; double changes in paraffin, one hour for each change), then embedded in paraffin (Paraplast with melting

point of 56°C). Five to seven micrometer thick sections along sagittal and transverse planes were cut on a microtome. The slides were then deparaffinized in 100% xylene (double changes, 2 minutes each), followed by the removal of the xylene with absolute ethanol (double changes, 2 minutes each). The slides were left in a Celloidin bath for two min. prior to transfer to 70% ethanol, then hydrated. After hydration, the slides were rinsed in distilled water for up to ten minutes, then stained with Harris's haematoxylin solution for three minutes. After being rinsed in distilled water, slides were washed under running tap water for 15-20 minutes, then transferred to 70% ethanol. The slides were then stained in alcoholic Eosin for ten seconds, dehydrated in 100% ethanol (three changes, each for two minutes), then transferred to 100% xylene (double changes, two minutes for each change). Finally, coverslips were mounted on to the slides using the mounting medium DPX. It has been demonstrated that this method provides the best staining of reproductive tissues of marine invertebrates (Mandryk, personal communication).

For transmission electron microscopy (TEM), anesthetized worms were fixed in 2.5% glutaraldehyde in 0.2M phosphate buffer (pH 7.6), followed by one hour fixation in 2% OsO_4 in 1.25% sodium bicarbonate at pH 7.2 (Wood and Luft, 1965). They were dehydrated in an ethanol series. Prior to being embedded in Medcast (Ted Pella, Inc.), the worms were cut into small pieces and only those pieces with a head and a few abdominal setigers were used. One-micrometer thick sections were stained with Richarson's stain (Richardson *et al.* 1983). Thin sections were mounted on uncoated copper grids, and stained with uranyl acetate and lead citrate, each for a period of 20 min.. Sections were examined with a Philips EM201 at 60KV.

C. RESULTS

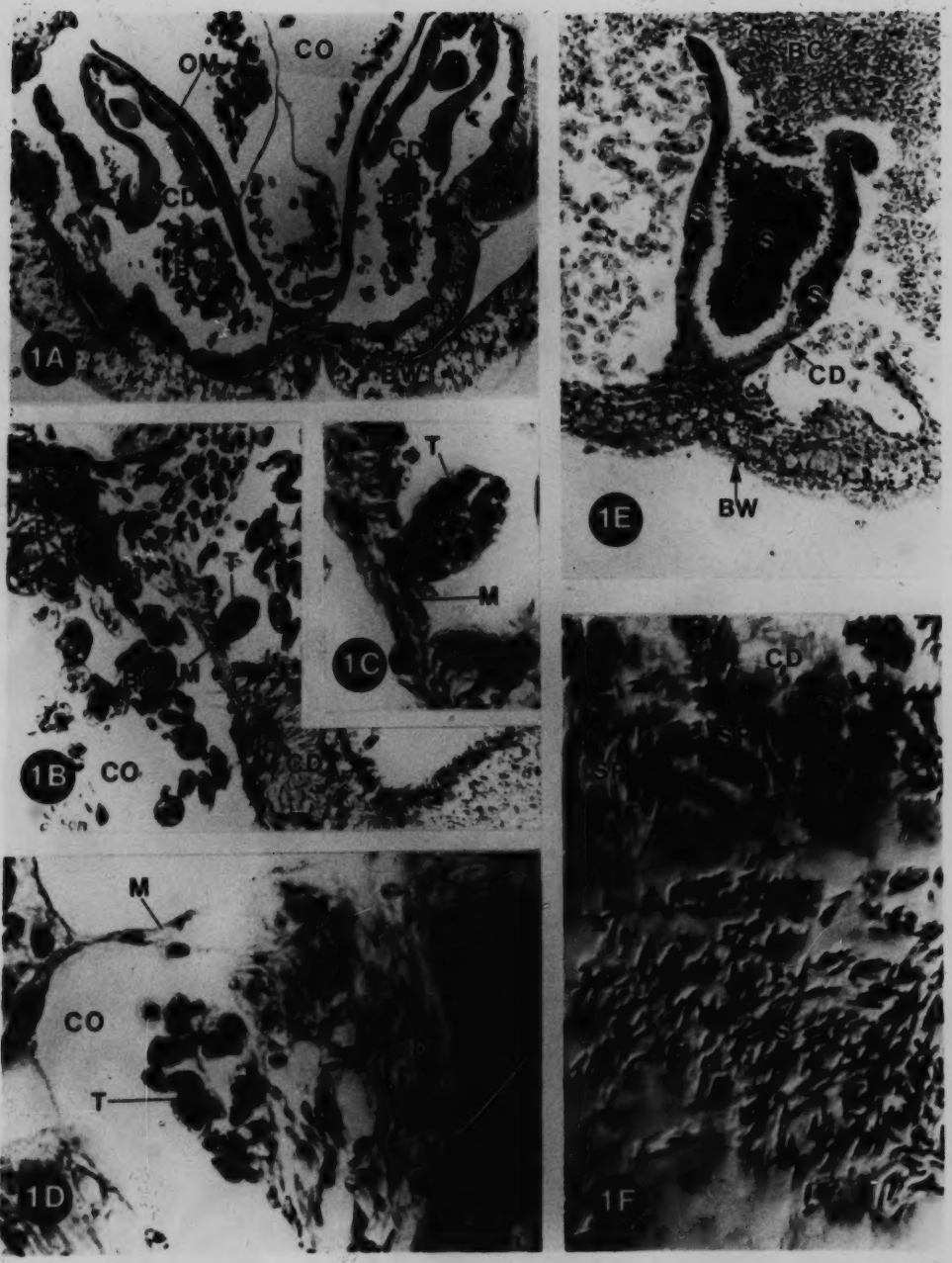
1. Light microscopy

Examination of "morphological females" indicated that all individuals that were older than 1.5 month possessed paired ovaries in the first 20 or more abdominal setigers. However, these individuals contained sperm while no copulating spines were found in any of these individuals when they reached sexually matured (indicated by spawning) at about 4 months old. Sperm were stored in one pair of coelomoducts located in the seventh and eighth setigers. Structurally, the distribution of the paired coelomoducts in the "morphological female" was identical to what has been described by both George (1984) and Eckelbarger and Grassle (1987) for males and hermaphrodites of *Capitella* spp.

The coelomoducts in 2 month old "morphological females" were trumpet-shaped structures; they were suspended in the ventral lateral part of the coelom by the oblique muscles and mesenteries (Plate 1A). At this stage, sperm were absent although ovaries were visible in the abdominal region. At the age of about 2.5 months, one pair of pear-shaped testes was found in setiger eight. The right testis was on the mesentery, between the tip of the right coelomoduct and the body wall, and the left testis was attached directly to the peritoneal membrane at the tip of the left coelomoduct (Plate 1B-D). Each of the testes was composed of a number of spermatocytes surrounded by a very thin membrane (Plate 1 C-D). It appeared that gametogenesis in the left testis was more advanced than that in the right testis, as some spermatocytes were seen outside of the testes (Plate 1C-D). Each testis measured about 35 micrometer in diameter.

In three month old individuals, the coeloms were filled with blood cells (Plates 1E). Mature sperm were found in the lumen of the coelomoducts as well as in the wall of the coelomoducts between setiger seven and setiger eight, and the ovaries were found in the setigers from segment 11 to 45. Thus, eggs must pass through mature sperm before being released to the outside of the body during oviposition. Large clusters of mature

Plate 1: Light micrographs of sections through the thoracic region of "morphological females" of *Capitella* sp. **A**. Cross section through the thoracic region of a ten week old individual showing paired coelomoducts (CD), the coelom (CO), nerve cord (N), body wall (BW), blood cells (BC), and oblique muscle (OM). 100X. **B**. Cross section of a 11 week old individual showing a small testis (T) from the right side of the coelom , mesentery (M), coelom (CO), blood cells (BC), and coelomoduct (CD). 1300X. **C**. Cross section through the right testis of a 11 week old individual (enlargement of B) showing the testis (T) and mesentery (M). 3200X. **D**. Cross section through the coelomoducts of a 11 week old individual showing a testis (T) from the left side of coelom, coelom (CO), mesentery (M), and coelomoduct (CD). 1300X. **E**. Section through a coelomoduct showing sperm (S) in the lumen of the coelomoduct and in the wall of coelomoduct; it also shows the coelomoduct (CD), body wall (BW), and blood cells (BC). 200X. **F**. Nomarski micrograph showing matured sperm (S) in the lumen of a coelomoduct; it also shows packed sperm (SP) in the colomoduct wall (CD). 2000X.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sperm in the coelomoduct wall (Plate 1 F) were noted, a phenomenon reported by George (1984).

2. Electron microscopy

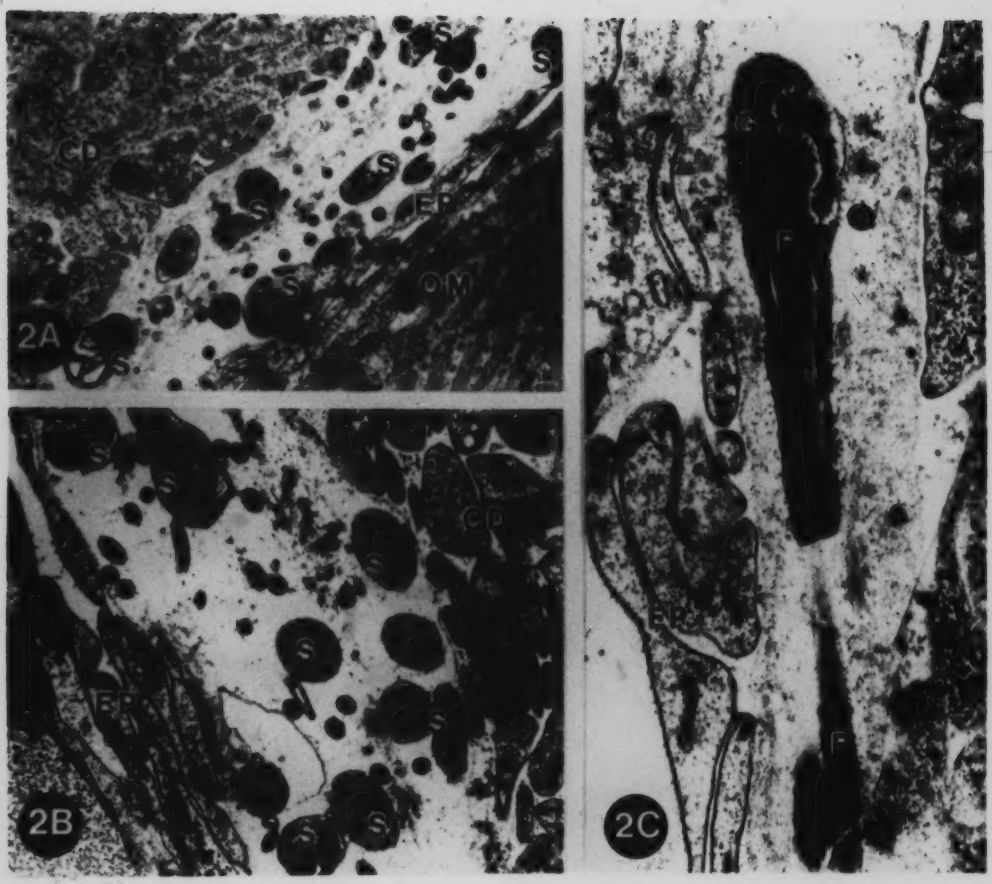
Spermatids were found in the epithelium of the coelomoduct in the region facing the coelom close to the oblique muscles (Plate 2 A-B). In this area, the epithelium of the coelomoduct was thin and was made of one or two layers of squamous epithelial cells. These cells appear to be identical to the epithelial cells of the oblique muscle bundle; both are derived from peritoneal cells (Plate 2 A-B).

More advanced spermatids were found in the outer layer of the coelomoduct; they are elongated cells with flagella positioned at the posterior end (Plate 2 C). Spermatids were also found in the coelom and in the lumen of the coelomoduct. The epithelial cells lining the lumen of the coelomoduct in the region closest to the body wall were columnar in shape; they had large basal nuclei and each cell was multiciliated and had many microvilli. The fine structures of mature sperm were similar to those that have been described in detail by Ecklebarger and Grassle (1987) for five sibling species of *Capitella*.

D. DISCUSSION

This report indicates that sex in *Capitella* is much more complicated than was previously suspected. Holbrook and Grassle (1984) reported that male *Capitella capitata* (species type I) developed into simultaneous hermaphrodites when reared in isolation or at low densities in the laboratory, and Petraitis (1985a, 1985b) found that the presence of females may inhibit male propensity to develop into simultaneous hermaphrodites in species type I of *Capitella capitata*. More recently, Petraitis (1988) demonstrated that hermaphroditism appeared when females were rare or when population densities were low, and suggested that feminization of males occurs when some males are unable to gain access to females. In the present study, the "morphological females" did not develop copulatory spines but did contain sperm.

Plate 2: Transmission electron micrograph (TEM) through the coelomoduct of "morphological females" of *Capitella* sp. **A**. Section through an area between the epithelium of the coelomoduct and the oblique muscle showing young spermatid (S) in the space of the epithelial cells (EP) of the coelomoduct (CD). Note also the oblique muscle (OM). 30100X. **B**. Section through an area between the epithelial cells (EP) of the coelomoduct (CD) and the oblique muscle showing the young spermatid (S) in the epithelium of the coelomoduct, arrows pointing at the cell-bridges of two spermatids. 31500X. **C**. Longitudinal section through a spermatid in the epithelia of coelomoduct, showing epithelial cells (EP), flagellum (F) and glycogen granules (G) of the spermatid. 25400X.


S
CP
EP
OM
2A
CP
EP
2B
F
EP
F
2C

The results of this study provide evidence challenging the conventional methods for determining the sex of capitellids. The presence or absence of copulating spines is no longer a reliable indicator of sexuality. Animals that do not have copulating spines could be either females or hermaphrodites.

Information on the testes and sperm production of *Capitella* is limited. All capitellids so far studied lack a well developed testes (George 1984, Eckelbarger and Grassle 1987). Eckelbarger and Grassle (1987) reported that young males have few specialized regions of the peritoneum in the eighth setiger, where germ cells proliferate and spermatogonia are released into the coelom where spermatogenesis takes place. In contrast, George (1984) reported that in *Capitella* sp. nov. mature sperm appear in the coelomic fluid and as large discrete clusters around the coelomoducts and give the appearance of being manufactured there. In *Capitella* sp. nov. (George 1984), *C. capitata* (Eisig 1887), and *C. hermaphrodita* (Boletzky and Dohle 1967), sperm platelets and rosettes were found in the coelomic fluid, which may also indicate that spermatozoa maturing in the coelomic fluid are accumulating in the tissue around the outside of the coelomoducts. All these studies were based on males or morphological hermaphrodites. In the present study, one pair of identifiable testes was found in young adults. The testes were associated with the epithelium of the coelomoduct. It is therefore reasonable to suggest that spermatogonia are developed in the testes, and then migrate into the outer layer of the coelomoduct and into the coelom. Spermatogenesis occurs in the coelom as well as in the wall of the coelomoduct. Sperm or spermatids developed in the coelom may finally be transferred to the lumen of the coelomoducts. Evidence shows also that sperm can develop and be stored in the wall of the coelomoduct .

The function of the coelomoduct of capitellids has been debated in previous studies. George (1984) suggested that the tissue of the coelomoducts is acting as a receptaculum seminis, based on the observation of bundles of sperm in the vesicles in the

tissue on the outside of the coelomoducts in *Capitella* sp. nov. In the same study, George (1984) also suggested that sperm may be manufactured in the coelomoduct. Eckelbarger and Grassle (1987) suggested that the coelomoducts simply act as collectors and storage of mature sperm, or may provide sperm with a nutritious microenvironment. My study provides morphological evidence to support the idea that the coelomoduct is one of the sites of spermatogenesis and may also function as the site of sperm storage. I believe that fertilization takes place in the coelomoduct when eggs are passing through the sperm in the duct during oviposition.

Previous studies have shown that only males are capable of developing into simultaneous hermaphrodites. Once a male develops into a hermaphrodite, it functions either as a male or female, and self-fertilization is rare (Grassle 1980, Holbrook and Grassle 1984, Petraitis 1985a, 1988). Mate competition among males has been considered as the major factor for the switching from male to hermaphrodite (Petraitis 1985a,1985b, 1988). This study does not support the above hypothesis as my evidence indicates that females are also capable of developing into a simultaneous hermaphrodites and that self-fertilization probably occurs in the lumen of coelomoducts.

In general, a hermaphrodite that developed from a female was similar to a male or a morphological hermaphrodite in sperm production. It may be more advantageous for a female to switch to a hermaphrodite than it is for a male, because a switch from a female to a hermaphrodite does not require the development of copulation spines, so that more energy can be put into the production of gametes. Since hermaphrodites can be self-fertilizing, they should be more adapted to an isolated environment or to areas of low population density. A single individual is capable of initiating a new population, which may explain why *Capitella* is distributed globally.

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CHAPTER VIII
GENERAL DISCUSSION

The present study demonstrates that even siblings of a single spawn of *Capitella* sp. can show great differences in growth rate, fecundity, egg size, egg energy content, and total reproductive output when reared under different food conditions, indicating that the reproductive characteristics of *Capitella* are flexible, and not conserved. Therefore, it is reasonable to suggest that reproductive characteristics are not reliable in the classification of sibling species among marine invertebrates. When sibling species of marine polychaetes such as *Capitella capitata* and *Polydora ligni* are classified, the impact of environmental factors on the reproductive characteristics should be considered.

This study shows that when *Capitella* sp. were reared in isolation under laboratory conditions, over 95% of the juveniles developed into "morphological females" and that all of their eggs developed normally. Examination of these animals with light and electron microscopes indicates that they were in fact functional hermaphrodites. This finding suggests that the conventional methods for distinguishing females and hermaphrodites in this group of worms are inadequate.

In the present study, great variations in fecundity, egg size, and adult size have been recorded in the field populations. Laboratory experiments have also demonstrated that reproductive variability can occur among the siblings from a single spawn. The results further indicate that even siblings of a single spawn can possess different responses to an identical environmental factor. As it was indicated in Chapter V, siblings of a single female from either a subtidal population or an intertidal population switched their growth rate, fecundity, egg size, and egg energy content when their diets were switched. This result supports the idea that the reproductive characteristics of these animals were environmentally controlled.

Capitella capitata is normally found in unstable environments. Therefore, the great variations in reproduction and growth of *Capitella* should be adaptive to accommodating these dynamic environmental conditions. Such uncertainty in environmental conditions may act as a driving force in the evolution of life-history traits in *Capitella*. It has been reported that opportunistic polychaete species (e. g., *Capitella capitata, Polydora ligni, Strobspio benedicti*), share many characteristics, including high flexibility in reproduction and growth, high sensitivity to environmental changes, and a great potential for converting energy into reproductive output.

Since the present study focuses on the impact of changing environmental conditions on the reproductive characteristics of *Capitella*, the taxonomic status of *Capitella* from my study area was not emphasized. I have included animals with three different developmental modes (planktotrophic developers from subtidal squid egg capsules, planktotrophic developers from intertidal mudflat, and lecithotrophic developers from intertidal mudflat) into a single group described as *Capitella* sp. Based on experimental results, I believe that animals with planktotrophic development (from subtidal squid-egg capsule and intertidal mud flats), may be the same species. However, it may not preclude that they are sibling species that have overlapping life-history characteristics. The relationship between animals with planktotrophic development and animals with lecithotrophic development need further investigation, although this study showed that some individuals can switch from one developmental mode to the other both under laboratory conditions as well as in the field, suggesting that they could be the same species.

However, future taxonomic studies may lead to a different conclusion. For instance, as adults, animals with lecithotrophic development can be distinguished from those with planktotrophic development by examining the ovaries. In lecithotrophic developers, each ovary carries fewer, but much larger ova. Lecithotrophic developers also have more setigers than planktotrophic developer. No distinct male was found in the

laboratory populations of lecithotrophic developers. On the other hand, individuals with planktotrophic development have both males and females and the sex ratio is almost equal to one.

In general, the taxonomic rankings of sibling species of marine invertebrates, (particularly in polychaetes), face severe challenges, because some of the characteristics used for classification are unreliable. The characteristics commonly used include fecundity, egg size, developmental modes, larval form, cross-breeding, sperm morphology, chromosome mapping, and isoenzyme studies. In addition, certain morphological characteristics of adults (e.g., size, number of setigers, morphology of setae) have also been considered. In the present study, it has been demonstrated that fecundity, egg size, and egg quality are highly variable within a population and are environmentally dependent; thus they are not reliable characteristics for distinguishing sibling species in *Capitella*. Great variations in fecundity, egg size, and offspring quality within the same species have been reported in marine invertebrates, fish, amphibians, and birds (see discussions in Chapters III,VI, V, and VI). Electron microscopic studies of the larval morphology of *Capitella* sp. have also indicated that the pattern of ciliation can vary among the sibling larvae from a single spawn (Qian, unpublished observation). It has also been demonstrated that two distinct larval developmental modes (planktotrophic and lecithotrophic) and life-history traits can coexist within a single polychaete species (Levin 1986, Levin and Creed 1986, Levin *et al*. 1987, Levin and Hugget 1989). Similarly, recent studies indicate that electrophoretic analysis may not be particularly useful in taxonomic studies because the electrophoretic patterns of a single species can be different, while different species can show similar electrophoretic patterns of some enzymes (Westheide 1989, Gosling and McGrath 1990). Crossbreeding experiments may be important in distinguishing between sibling species. Unfortunately, crossbreeding experiments could not be conducted in the present studies because of the

difficulty in distinguishing real females from "morphological females" (hermaphrodites) in the animals that had lecithotrophic development.

The validity of using morphological characteristics in polychaete taxonomy has also been debated. For example, the morphological features of setae have been most heavily used to separate sibling species or closely-related species. However, a recent study of *Prionospio japonica* showed that there can be more than 28 morphological variations of the hooded hooks of a single specimen (Ohwada 1989).

Many authors have suggested that larger eggs often give rise to larger offspring that are more competitive for food, less vulnerable to predation, and better adapted to compete for space (Bagenal 1969, Gall 1974, Spight 1975, Kraeuter *et al.* 1982, Marsh 1986, Marteinsdottir and Able 1988, Rhymer 1988, Williamson and Bull 1989). Thus, at times when food is in low supply and when juvenile density is high, or when there is high predation pressure on the juveniles, females that have the potential to produce larger eggs are selected for, in order to produce larger and competitively superior juveniles (Smith and Fretwell 1974). Chia (1974) suggested that marine invertebrates tend to produce fewer and larger eggs when food is limited, and produce more and smaller eggs when food is abundant; the trade-off between the two modes of reproduction appears to be between the higher survival rates (fewer but larger eggs) and greater dispersion (more but smaller eggs). I believe that changes in egg size are responses to environmental condition. Under some conditions, a larger egg is expected to do better than a smaller, but under other conditions the small egg would have a greater fitness. Therefore, animals that produce a wide range of eggs would be more adaptable to a dynamic environment. Kaplan and Cooper (1984) also suggested that a single female can produce eggs of very different sizes at different times or two genetically similar females can produce eggs of very different sizes at the same time if they have different environmental histories. My results in the present study appear to support these predictions, since "trade-offs" between fecundity and egg size have been demonstrated in several sets of experiments.

For example, when sibling animals were provided with different quantities of food, their fecundity was correlated with the amount of food, while egg size decreased (see Chapter IV). Although siblings that were fed squid egg capsules and those that were fed ground *Ulva* invested similar amounts of energy in their eggs, they showed two distinct, separate life-history traits. Individuals fed on squid egg capsules produced seven to eight times more eggs that were smaller and contained less energy. Those fed on ground seaweed produced fewer eggs that were larger and contained more energy (see Chapter V). However, these two different life-history traits can be switched by switching the food conditions. In addition, animals that were fed smaller amounts of food or that were starved, often produced fewer, but larger, eggs than those that were fed a large amount of food. Hughes and Roberts (1980) found that the marine snail *Littorina rudis* under high predation pressure from crabs at one site produced larger eggs and, hence, larger juveniles; at another site with no predation the snails had greater fecundity with smaller eggs. Larger eggs are also associated with conditions of high desiccation. Etter (1989) found that individuals of the snail *Nucella lapillus* in exposed shore deposited twice as many egg capsules hatchlings as those from protected shore and eggs from exposed shore contained less energy and developed to smaller hatchlings than those from protected shore.

There is also a trade-off between other life history characteristics among animals of the two developmental modes. Under similar laboratory conditions, animals with planktotrophic development reached sexual maturity earlier and had higher fecundity, but had smaller eggs and shorter generation times than animals with lecithotrophic development. They also had shorter life-spans, with higher larval and adult mortality. In terms of the life-time net reproductive output, the animals with planktotrophic development were similar to those with lecithotrophic development.

Poecilogony (polymorphic development) in marine invertebrates has received considerable attention in recent years. A literature review indicates that poecilogony can

occur in any of the following situations: (1) the same species produces different-sized eggs or embryos, (2) there is geographical variation between populations of the same species, and (3) when there is distinct seasonality of the biological environment (e. g., amount of food available to the parent). After analyzing 64 species of molluscs and polychaetes that have been reported to be poecilogous, Hoagland and Robertson (1988) concluded that seasonal and geographical variations in development were due to the cryptic species involved and that developmental pattern was generally a reliable species character in invertebrate systematics. They argued that great intraspecific variability in other reproductive characters (e. g., brood size, fecundity, age at maturity, and sometimes, egg size) all reflect quantitative differences, whereas poecilogony is a qualitative difference that involves ecological as well as morphological differences. This conclusion can be misleading because changes in quantity can often lead to changes in quality. For example, many studies have demonstrated that changes in egg size often result in differences in offspring fitness (e. g., larval size, hatching time, larval feeding capacity, resistance to harsh environments,etc.).

Hoagland and Robertson (1988) suggested that poecilogony can only be proved when interbreeding occurs between individuals with different larval types, or when a single individual observed in the laboratory produces two types of larvae under varying environmental or nutritional conditions, or when cross-breeding occurs among normally allopatric populations, combined with allozyme or other molecular genetic studies. Gibson and Chia (1989) found that in a single egg mass of the opisthobranch *Haminoea callidegenita,* two kinds of offspring are produced: a veliger or a juvenile and this poecilogony is determined to a certain extent by the presence or absence of egg mass jelly. Blake and Kudenov (1981) found that *Boccardia proboscides* produces two larval types within a single egg capsule -- one that is capable of feeding in plankton and another that feeds on nurse eggs and smaller larvae in the egg capsule. George (1967) found that a single brood of the polychaete cirratulid *Cirriformia tentaculata* contained both free-

swimming and demersal larvae (all lecithotrophic) that were morphologically identical. Levin *et al.* (1987) suggested that the polymorphic development (the lecithotrophic and planktotrophic developments) of *Streblospio benedicti* is irresponsable to environmental conditions. Levin *et al.* (1987) showed that both planktotrophic and lecithotrophic developments had high population growth rates, but the former through a fecundity advantage, the latter through a survival advantage early in life.

In my study, siblings that developed from a single spawn showed great variation in fecundity, egg size, and egg energy content when they were fed on different kinds of diet, or produced both planktotrophic and lecithotrophic larvae when they were fed on different rations of food or starved; this indicates that *Capitella* sp. studied here can also be poecilogous. These results further support the theory of the ecological plasticity of reproductive mode proposed by Thorson (1950).

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